UNIVERSITY OF EXETER

DOCTORAL THESIS

What mechanisms have produced a self-regulating Earth system?

Submitted by Arwen Elizabeth Nicholson to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Geography in June 2019

Signed: _____ Date: _____

"The idea that we are 'stewards of the Earth' is another symptom of human arrogance . . . The Earth will live on until the sun dies – it's just a question of whether we'll be a part of its future."

Lynn Margulis

UNIVERSITY OF EXETER

Abstract

College of Life and Environmental Sciences
Geography Department

Doctor of Philosophy

What mechanisms have produced a self-regulating Earth system?

by Arwen E. NICHOLSON

The Gaia Hypothesis postulates that life and the oceans, crust, and atmosphere of the Earth form a self-regulating planetary-scale system with stabilising properties. Gaia helps to explain the long history of uninterrupted habitability on Earth. Previous Gaian models have uncovered mechanisms for self-regulation in life-environment coupled systems, such as the Earth, and the work in this thesis adds to our understanding on how and when self-regulation can emerge on a planet hosting life, and what conditions help maintain such regulation once established. To place the models presented in this thesis into their proper context this thesis contains background on Earth's history, the history of the Gaia hypothesis and some key Gaian models and known Gaian regulation mechanisms, and a discussion on habitability of exoplanets and our search for alien life.

In this thesis I explore a new variant of a pre-existing Gaian model (the flask model) which demonstrates a new regulation mechanism which I call 'single-rein control'. I then adapt this model to explore the hypothesis of 'selection by survival'. This hypothesis suggests that the longer a life harbouring planet survives, the longer it has to acquire further persistence mechanisms. Therefore over time the only planets hosting life still existing will be those that have acquired several self-regulation mechanisms like those present on Earth. The results of this model demonstrate that selection by survival can promote long term persistence of biospheres compared to a null model.

In the second part of this thesis I consider how the Gaia hypothesis can inform our search for inhabited exoplanets and I introduce the ExoGaia model, a new model of atmospheric regulation where microbes must 'catch' a window of habitability on their host planet, and quickly form self-regulating feedback loops to prevent the planetary temperature from rising to inhospitable levels.

The ExoGaia model demonstrates global regulation and the underlying geochemistry on the planet turns out to be key in determining how robust this regulation is. ExoGaia also demonstrates 'Gaian bottlenecks' where for the same planet life either quickly establishes self-regulating feedback loops and enjoys long term habitability, or fails and becomes extinct, with the host plane quickly reverting to an inhospitable state. This model agrees with the hypothesis that inhabitance and habitability are two sides to the same coin – that a planet is highly unlike to be in a habitable state, without being inhabited.

This thesis argues a case for 'Probable Homeostatic Gaia' – that not only is the Earth-system homeostatic but that homeostatic regulation is an expected result of a life-environment coupled system. If true, this would would increase our chances of finding other Gaian worlds.

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In this thesis I remember my grandparents, most of whom are sadly not here to read this work. My nanna who gifted me my lifelong companion

Teddy, my grandad the engineer who kept a copy of my first ever published scientific paper until the day he died, my grandad who encouraged me towards science with experiments including a failed attempt to grow crystals (the resulting strange orange non-crystals lived on for years proudly displayed in a jar), and I thank my Nanny who shares my love of our beautiful wildlife.

So much thanks is owed to my Mum and Dad for their endless support. From the moment I was born they instilled in me a wonder of the world, and a drive to discover more about our amazing universe. Their contagious enthusiasm for science has lead the 3 year old who sobbed "Gravity pulled me down!" when she fell, to become the author of this thesis.

My sisters and partners in crime have been a lifeline during my studies. Rhana has been an invaluable ally whilst we have gone through our PhDs together. That camaraderie has kept my spirits up throughout and our near weekly Skype rants have kept me sane through the process of writing up this thesis. Elara helped cement my desire to turn my research towards exoplanets when she provided me with the opportunity to visit ESA's mission control centre (and talk to the Gaia telescope!). She has often visited me in Exeter bringing with her Oatly Foamable and her incredible cooking skills.

Without Rudy I might never have applied for this PhD let alone written this thesis. He has always believed in me. He has spent countless hours discussing my research with me and proof reading my work. I am endlessly grateful for his love and support.

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Publications

Parts of this thesis have been previously published in journal articles and conference proceedings:

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Nicholson, A. E., Wilkinson, D. M., Williams, H. T. P., and Lenton, T. M. (2018). Alternative Mechanisms for Gaia. *Journal of Theoretical Biology*, 457, pp249-257

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For my family. . .

Overview of this Thesis

Welcome to my thesis!

The question posed by this thesis title is: "What mechanisms have lead to self-regulating Earth system?" and I hope the work presented adds to our ability to answer this question. It has been well accepted for some time now that the Earth does have self-regulatory feedback cycles that involve life, and that life has had a large hand to play in shaping our world. The Earth is a vast complicated ever changing system, and no computer model can mimic it in its entirety and the models presented in this thesis don't even attempt such a feat. Here I focus on highly abstract simple representations of key processes occurring on Earth. Focusing on such models allow me to clearly understand how the models are functioning and to precisely determine any regulation mechanisms that emerge. With this in mind the following results are by no means directly applicable to the Earth however the essence of what they tell us about life-environment coupled systems can help shed light on how our living planet has self-regulated for so long.

This thesis is roughly organised into two parts. The first part consists of chapters 1 - 5 and covers earth history, the history of the Gaia hypothesis and various Gaian models, and then work published from research done during this PhD, exploring a new regulation mechanism 'single-rein control', and a selection mechanism, first described as a thought experiment (Doolittle, 2014), but explored computationally for the first time in this thesis. This part of the thesis is highly Earth-centric.

The second part, Chapters 6 and 7 look beyond Earth's horizons and ask how the Gaia hypothesis can inform our search for habitable exoplanets and alien life. Results from published work show that depending on how successful early life is in colonising its host planet, it could drastically steer the course of its host planet's evolution. This work demonstrates so called 'Gaian bottlenecks' (Chopra and Lineweaver, 2016) where early in a planet's formation life must emerge and quickly establish self-regulating feedback loops in order to 'catch' the habitability window on their planet and maintain said habitability for long timespans.

1 Layout of this thesis

Chapter 1 - A Brief History of Earth

In this chapter I give a quick overview on the formation of our planet, the first life on Earth, and some of the major transitions that have occurred since life appeared on the scene. This chapter does not yet mention Gaia but rather sets the scene for the hypothesis.

Chapter 2 - Introducing Gaia

In this chapter I introduce the Gaia hypothesis and briefly cover the history of the hypothesis, variations on the hypothesis and where the general scientific consensus is today. Discussing Gaia will shed new light on some of the historical events discussed in the previous chapter on Earth history.

Chapter 3 - Gaian Models

This chapter gives a summary on some of the key Gaian models most relevant to this thesis. Although Daisyworld does not feature in this thesis, as it was the first Gaian model and thus a key part of Gaia history, and so I give a brief description of the original model, and some of its variants.

Chapter 4 - The Single-Flask Model

This chapter explores a model of a microbial biosphere living in a zero-dimensional world that consists of chemicals they may consume and excrete as part of their life processes, and also a global temperature which is impacted by microbial metabolisms. This chapter gives an overview on the 'single-Flask model' and explores the results from this model, namely the regulation mechanism that emerges - single rein-control.

Chapter 5 - Alternative Mechanisms for Gaia

In this chapter I explore the hypothesis of 'selection by survival' (Doolittle, 2014) using an adapted single-flask model. Rather than focusing on regulation mechanisms as in the previous chapter, here I focus on selection mechanisms for Gaian systems. The results from this work demonstrate

that selection by survival can indeed increase the survival prospects of life-environment coupled systems over a null hypothesis of a constant rate of total extinction.

Chapter 6 - Habitable Exoplanets and Alien Life

This chapter gives a brief summary on the huge area of research in exobiology and exoplanet research. I briefly cover the potential past and present habitability of other planets in our solar system than Earth (e.g. Mars, Venus), cover how habitable zones around stars are defined and how an understanding of Gaia can help inform such definitions, and give a brief overview on the exoplanets discovered to date and their potential habitability, all bearing in mind that as we only have the Earth to go on our search for alien life is inherently biased by Earth.

Chapter 7 - The ExoGaia Model

This is the longest chapter in this thesis by far. Here I present a new model of atmospheric regulation by evolving microbial biospheres called the ExoGaia model. It expands on previous models by have the microbes regulate a chemical atmosphere, the composition of which determines the surface temperature on the planet which in turn affects the fitness of the microbes.

Chapter 8 - Conclusions

The summary and conclusions of the work presented in this thesis and what I think the next steps are in understanding Gaia and how this understanding applies to our search for inhabited alien planets.

2 Before we begin...

Any work on Gaia will inevitably span many topics as a look at our living planet incorporates geology, geochemistry, biogeochemistry, biology, evolution, physics, maths and more. I have hopefully introduced each concept in an accessible way so that readers need not be experts in any area to follow the work in this thesis. My own background before commencing this PhD was largely in maths and physics and so I had much to learn about biology, geology and chemistry in order to produce the work you are about to read.

This thesis heavily focuses on highly abstract simplified representations of life-environment coupled systems using agent based dynamics over discretised differential equations. My hope is that the key assumptions and processes coded into my models are simple enough to follow so that it is fully appreciated that the regulating behaviour exhibited by these models is an emergent properly, and not something hardwired into my model worlds.

Throughout this thesis I have incorporated diagrams showing how the models presented are designed and how the regulation mechanisms they demonstrate function so as not to overly rely on mathematical equations to describe the key elements of this work. I have also tried to include a great variety of images to emphasise and compliment the points I make. They say a picture is worth a thousand words, and they certainly brighten up a page if nothing else. I hope you find this thesis readable and dare I say enjoyable!

Chapter 1

A Brief History of Earth

To begin, I will provide a brief history of planet Earth. This thesis does not directly address specific events in our planet's history, however these events inform the design of the models developed in this thesis. Results from these models can then in turn inform research into the driving mechanisms of these events, and so an overview is useful to introduce ideas and events that will be mentioned in later parts of this thesis. A lot has happened on Earth since its formation, and I will only give a quick overview of some highlights where it relates to my work. This chapter is by no means an in-depth overview of the history of our planet. A timeline summary of what is discussed in this chapter is provided at the end in Figure 1.6 to help show when events occurred in relation to each other. This Chapter will be entirely Earth-centric; a discussion on the habitability of other planets is found in Chapter 6.

1 The Early Earth

The Earth formed roughly 4.54 Gya (billion years ago) (Dalrymple, 2001) at the same time as the formation of our Sun and solar system. Our solar system is thought to have started in an open cluster – a large dust cloud where stars are born. Asymmetries in the gas causes clumping with these 'clumps' then accumulating more gas until densities are high enough for objects, such as stars, to be born. As the matter that would become our sun was accreting, matter in the disk surrounding this dense centre also clumped and formed the planets of our solar system, including Earth (Podosek and Cassen, 1994). Earth's moon is thought to have been formed from an impact with a Mars sized planet, sometimes named Theia after the Greek mythological mother of the moon (Halliday, 2000), and the proto-Earth roughly 4.5 Gya (Canup and Asphaug, 2001).

The Earth just formed would have been an extremely hostile place, with temperatures far too high for any known life and no solid crust, and the new

planet would have experienced frequent collisions with large objects. This period has been named the 'Hadean' eon evoking the hellish conditions at the time. It was initially thought that a solid crust didn't form on Earth until about 3.8 Gya as no rocks older than this date had been found (Stevenson, 1983), however rocks predating this cutoff have since been found (Bowring and Williams, 1999), and models predict that the Earth would have cooled far more rapidly, in the order of only 10 million years after the impact that formed Earth's moon (Sleep, 2010). Studies of zircons suggest that some continental crust formed as early as 4.4 Gya – very soon after the Earth's formation – and the 'cool early Earth' hypothesis suggests that condition that would allow liquid water oceans on Earth existed from 4.4 - 4 Gya (Valley et al., 2002).

The late heavy bombardment (LHB) (Tera, Papanastassiou, and Wasserburg, 1973; Tera, Papanastassiou, and Wasserburg, 1974; Claeys and Morbidelli, 2011) is hypothesised to be a short period of time between roughly 4 - 3.95 Gya when Earth was frequently suffering large impacts from comets and leftovers from terrestrial planet accretion (Nesvorný, Roig, and Bottke, 2017). Evidence for the LHB comes from lunar samples collected during the Apollo missions. Dating of the samples implied that most of the impact melts occurred within a short span of time and thus that the Moon experienced a short spike of intense bombardment (Jessberger et al., 1974; Turner and Cadogan, 1975). If such a spike in impacts occurred on the Moon, then Earth, Mars and other inner solar planets would also have experienced this bombardment.

During the LHB, the surface of the Earth would have been repeatedly destroyed, vaporising oceans and rocks on the surface, however recent research suggests that this surface destruction was not complete and the Earth was never sterilised (Abramov and Mojzsis, 2009) meaning that any microbial life alive during this time is likely to have survived. This could explain why rocks older than 4 billion years are uncommon. From roughly 3.8 Gya the hypothesised bombardment is thought to have ended and it is well accepted that there were surface oceans on Earth, tectonic activity and that the planet was in a habitable state.

Doubt has been cast however as to whether the LHB occurred. Models of early solar system formation struggle to achieve the short heavy influx of asteroids corresponding with the supposed dates (Nesvorný, Roig, and Bottke, 2017), and it is possible that some of the Apollo lunar samples are actually from older impact events that became contaminated by material from

later events, thus producing a younger age and leading to each crater site sampled appearing to be of the same age (Spudis, Wilhelms, and Robinson, 2011). An alternative hypothesis is that the rate of impact from comets and asteroids was initially high after the formation of the solar system and that evidence taken for the LHB actually marks the decline after a long history of bombardment (Chapman, Cohen, and Grinspoon, 2007).

The first atmosphere on Earth was formed from the accretion of gases from the solar nebula while the Earth was forming and was probably similar in composition to the atmospheres of the gas giants Jupiter and Saturn, mostly H_2 (Zahnle, Schaefer, and Fegley, 2010). Earth's secondary atmosphere was formed mostly via outgassing from volcanoes, with some additional gases delivered by the comets and asteroids during LHB if it occurred. It mostly consisted of H_2O, CO_2 and N_2, with small quantities of CO and H_2 (Zahnle, Schaefer, and Fegley, 2010). Biologically important CH_4 would have formed in low quantities (Tian et al., 2005). Importantly, the early atmosphere was devoid of oxygen, and O_2 levels would not rise on the planet until some time after the evolution of oxygenic photosynthesis (see Section 2 .2).

Without abundant atmospheric oxygen, Earth's early oceans were rich in dissolved iron provided via convection from the Earth's mantle (Walker and Brimblecombe, 1985). This contrasts to the oceans today which are iron poor due to most of the iron released from deep sea hydrothermal vents either quickly reacting with dissolved sulphide and being deposited nearby, or being oxidised to ferric (oxyhydr)oxide minerals (Poulton and Canfield, 2011), which are not water soluble.

Plate tectonics are accepted to have been present during the Archean eon (beginning 4 Gya and ending 2.5 Gya), although caused by different mechanisms to the ones driving them today (Sleep and Windley, 1982), and evidence suggests the presence of tectonic activity even earlier during the Hadean (Hopkins, Harrison, and Manning, 2008). Recycling of the ocean crust was occurring. The plate tectonic mechanisms that dominate today have been present since at least 1.89 Gya (Group, 1990), late in the age of the Earth on a geological timescale. Importantly however, abiotic mechanisms for recycling surface materials seem to have been in place since around the time life began.

Into this world, alien and uninhabitable to us, life emerged, took hold, and flourished.

1 .1 The first life on Earth

The Last Universal Common Ancestor (LUCA) is a hypothesised organism that is the common ancestor of all life on Earth (Crick, 1968; Sober and Steel, 2002; Sober, 2008), first postulated by Darwin (Darwin, 1859). Evidence backs up the likely existence of LUCA (Theobald, 2010), however this does not mean that life emerged only once; there may have been multiple origins of life with all but one going extinct (Raup and Valentine, 1983). It is currently thought that life on Earth has descended from an 'RNA world' where self replicating RNA molecules existed before DNA or proteins evolved (Copley, Smith, and Morowitz, 2007; Neveu, Kim, and Benner, 2013), although this RNA world may itself have been preceded by another self-replicating molecule (Robertson and Joyce, 2012). The first fossilised evidence for life is prokaryote life – cells with no nucleus.

An exact date for the first life on Earth is unknown. The earliest proposed direct evidence for life (fossilised prokaryote cells) comes from 3,465 million year old rocks from the Apex chert deposit in Western Australia (Schopf et al., 2017). Of the 5 prokaryote species studied from this rock, two were inferred to be early photosynthesisers, one a methane producer, and two others methane consumers. Schopf et al. (2017) write that this discovery is consistent with the RNA world hypothesis and suggests that methanogen/ methanotroph microbe communities were a large component of the biosphere of early Earth. This interpretation of these rock formations as fossils is contested however, Brasier et al. (2002) for example think it more plausible that the supposed fossils are actually abiotic hydrothermal artefacts. Possible earlier evidence comes from the isotopic composition of carbonaceous materials which is indicative of life. Evidence for life has been found in rocks interpreted to be seafloor hydrothermal vent-related precipitates, dated between 3,770 - 4,290 Mya (million years ago) (Dodd et al., 2017) and life on land may have existed as early as 3.5 Gya (Djokic et al., 2017).

During the late heavy bombardment (LHB), if it occurred (see Section 1), surface habitats on Earth would have been repeatedly destroyed (although total sterilisation is not thought to have occurred (Abramov and Mojzsis, 2009)), but these large impacts may have created new subsurface habitats in the form of hydrothermal systems (Zahnle and Sleep, 1997) which could have sheltered life, or perhaps even have been the birthplace of the first life on Earth (Baross and Hoffman, 1985). The Grand Prismatic hot springs in Yellowstone National Park USA is a possible modern day example of such a haven for early life, see Figure 1.1. It also demonstrates how habitability is

dependant on what life form we are considering. While thermal springs may have been the cradle of life, they are highly hostile to more complex later life-forms, such as the people visiting the Grand Prismatic in Figure 1.1. Dip a tourist in the hot spring and they would not find it at all hospitable!

Evidence suggests that our last universal common ancestor, LUCA, was thermophilic or hyperthermophilic in nature, meaning that the LHB may have created an impact-induced thermal bottleneck for any life on Earth at the time (Gogarten-Boekels, Hilario, and Gogarten, 1995). This means that to persist during this time, life had to survive extremely high temperatures, any life that could not went extinct. The current dates held for the first life on Earth show that life either emerged before (Betts et al., 2018), or during, the LHB and survived this volatile time period, or it arose soon afterwards. If the LHB did not occur, the comparatively 'gentle' impact history the Earth experienced instead would have posed far less of a challenge to life.

FIGURE 1.1: Hot springs like the Grand Prismatic in Yellowstone National Park USA, pictured here, provide a glimpse of what the world might have been like for early life. Photo credit: Elara Nicholson

It is generally well accepted that life has been present on Earth for at least 3.5 billion years. Eukaryotic life is thought to have evolved on Earth around 1.5 Gya (Semenza, 2007), and animals appeared on the scene by 558 Mya (Bobrovskiy et al., 2018), followed by the Cambrian explosion around 541 Mya (Smith and Harper, 2013). We've only been around for 2 million years (Alemseged, Coppens, and Geraads, 2002), not long at all in terms of Earth history! To put this in perspective, imagine the Earth has only existed for 24 hours. On that timescale, humans only appeared on the scene one second ago!

Whenever life began, it began early in Earth's history, from the earliest that sedimentary rocks can be reliably dated, signs of life are also found. Once emerged, life has persisted uninterrupted. We can use the evidence that

life started quickly once conditions became habitable, and that all life shares a universal ancestor, to inform the rules of models exploring life-planet interactions.

2 Perturbations on our planet

Earth's 4.54 billion year history has been far from uneventful. From its birth to now, the Earth has undergone drastic changes in surface conditions – from a planet we humans would consider an inhospitable alien landscape, to the world we live in today. During its long existence, life has had to survive a number of large-scale changes on Earth, such as snowball Earth events – where the whole planet is theorised to have been covered in ice from poles to equator, or the rise of atmospheric oxygen in a previously anoxygenic world. I will now give a brief overview on some key events in Earth's history that are discussed in this thesis.

2 .1 Our changing Sun

Our Sun is a main sequence star – it generates the thermal energy we depend on to survive via nuclear fusion of hydrogen to helium. It is roughly halfway through its main-sequence stage; after roughly 5.5 billion years when the hydrogen in its core is exhausted, it will expand rapidly to become a Red-Giant and burn shell hydrogen, and core helium for fuel (Schröder and Connon Smith, 2008). During its time on the main-sequence, the sun has been gradually warming (Gough, 1981). This is due to the helium atoms created taking up less space within the sun than the hydrogen atoms they were formed from. This causes the core to shrink and the sun to become denser and this in turn causes more gravitational pull on the outer layers of the sun, increasing the pressure near the core which speeds up fusion. Before the Sun becomes a Red-Giant, its luminosity will have nearly doubled from today's value (Schröder and Connon Smith, 2008), and Earth will be receiving as much sunlight as Venus does today. When the Sun becomes a Red-Giant, it will expand in size, large enough to engulf Mercury, Venus, and likely Earth. Figure 1.2 shows how the temperature, luminosity and radius of the Sun has changed in the past, and is expected to change in the future, with respect to its present day values (Stix, 2002; Ribas, 2009).

Back when life emerged on Earth, roughly 3.8 Gya during the Archean, the Sun had a luminosity of around 70% of its present day level (denoted

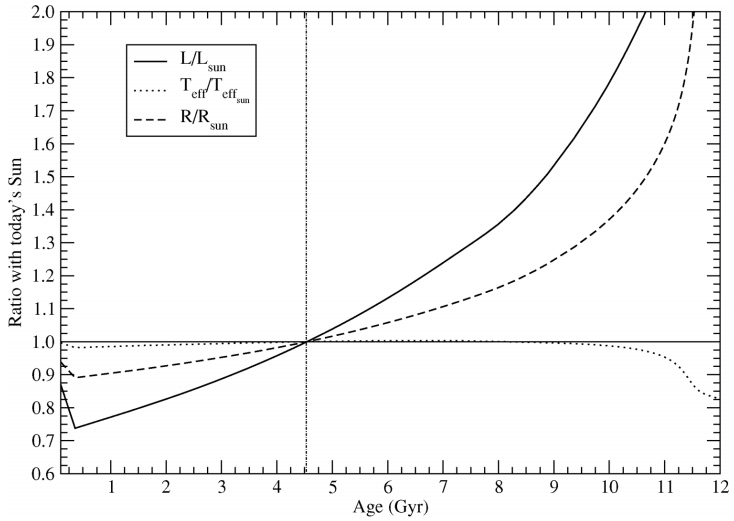


FIGURE 1.2: Plots showing the luminosity, temperature and radius of the Sun over time, with respect to present day values. Image from (Ribas, 2009)

as $L_{\odot}$). This suggests a cold early Earth. With today's atmosphere, a solar luminosity of $0.7 \times L_{\odot}$ would be too cold for liquid surface water on Earth; the Earth would be under permanent global glaciation (Lenton and Watson, 2011). However evidence shows that for the past 4.4 Gya (Valley et al., 2002), the Earth has had surface conditions allowing for the presence of liquid water. This is known as 'the faint young sun paradox' (Sagan and Mullen, 1972).

Models suggest that to maintain liquid water at the surface under such conditions, CO_2 levels would have had to be 400 times higher than the present levels. It was assumed that lower levels of carbon burial happening at this time were responsible for the build up of CO_2 (Own, Cess, and Ramanathan, 1979; Walker, Hays, and Kasting, 1981). However, evidence from a range of sources put an upper cap on the levels of CO_2 from between 3.5 - 2.2 Gya, that would be insufficient to counter the early faint sun.

2.75-2.2 billion year old 'palaeosols' – preserved soil samples – provide an upper limit on CO_2 levels during that time that are are lower than the levels that climate model suggest would be needed for sufficient warming (Rye, Kuo, and Holland, 1995). Caps on CO_2 levels for earlier times come from 3.2 billion year old river gravel (Hessler et al., 2004) and 3.5 billion year and 3.2 billion year old evaporites (Lowe and Tice, 2004). Models also suggest that such high CO_2 levels would not have been possible to maintain during the Archean due to rapid CO_2 removal by carbonation of the oceanic crust and tectonic loss to the mantle (Sleep and Zahnle, 2001). Other models suggest

that the lower albedo of the Earth during the Archean would have counteracted the fainter sun at the time, removing any requirement for a very strong greenhouse atmosphere (Rosing et al., 2010).

Methane has since been suggested as playing a key role maintaining a high temperature during the Archean, with a higher concentration helping to keep the Earth in an unfrozen state (Lovelock, 1988; Pavlov et al., 2000). A lower albedo of the Earth due to less continental land area, combined with a lack of biologically induced cloud condensation nuclei (Kump and Pollard, 2008) has also been suggested as an explanation for Earth's warmer than expected past temperatures (Rosing et al., 2010).

Over time, the levels of atmospheric CO_2 and CH_4 have decreased, causing a smaller greenhouse effect, and thus balancing the increasing luminosity of the Sun and avoiding the runaway greenhouse that occurred on our neighbour Venus. There are abiotic mechanisms whereby an increase in global temperature leads to a decrease in greenhouse gases, for example the increased rate of silicate weathering with warmer temperatures which in turn increases burial of atmospheric CO_2 as carbonates (Brady and Carroll, 1994). However it now seems likely that biology has played a role in maintaining the continued life-friendly surface temperature on Earth in the face of a warming host star (Lenton, 1998), see Chapter 2.

The less luminous early sun also has habitability implications for our neighbouring planets – Mars and Venus. With a cooler sun, might early Venus have been habitable? As Mars today is dry and cold, with an even cooler past sun it would be expected that early Mars would have been colder than today. However evidence shows that liquid water once ran on the surface of Mars implying warmer temperatures and thus a thicker atmosphere. These questions are revisited in later Sections 6 and 7.

2 .2 The rise of oxygen

Before the evolution of oxygenic photosynthesis, the level of O_2 in the Earth's atmosphere was very low, of the order of one part per trillion (Lenton and Watson, 2011). This is in stark contrast to present day Earth – today oxygenic photosynthesis (OP) releases oxygen into the atmosphere in vast quantities (around 300 billion tons annually (Lenton and Watson, 2011)) and O_2 accounts for nearly 21% of our atmosphere. At first glance it might appear that the high rate of OP can explain our highly oxygenated world. However,

atmospheric O_2 levels are roughly stable, therefore some process must be removing O_2 at the same rate as it is produced, otherwise the concentration would quickly rise, or fall. Atmospheric O_2 can only increase if the reductant that is buried to produce it does not later return to the atmosphere thus cancelling out any O_2 gains (Hunten and Donahue, 1976). The rise of oxygen from early levels to today's, is thought to have occurred in several steps (Canfield, 2005), with two being much more significant than the rest (Kump, 2008).

'The Great Oxidation event' (GOE) is a period of time between 2.45 and 2.22 Gya (see Figure 1.3) where atmospheric oxygen levels rose significantly. This event could have been a direct consequence of the evolution of oxygenic photosynthesis (OP) (Kopp et al., 2005), however evidence strongly suggests that O_2 producing lifeforms pre-date the Great Oxidation Event (Brocks et al., 1999) by >250 million years. Atmospheric O_2 levels remained very low, below a few parts per million (Kasting and Ono, 2006) during this time, although evidence indicates that small amounts of O_2 were present 50 million years before the GOE (Anbar et al., 2007). If OP pre-dates the GOE, then the GOE would have to have been the result of a change in the balance of oxidants and reductants on the surface of the Earth.

The delay between the evolution of OP and the GOE is thought to be due to bi-stability in the atmospheric concentration of oxygen. Low levels of oxygen are stable until, at a certain point, a rapid transition to a high oxygen state occurs. A model by Goldblatt, Lenton, and Watson (2006) shows that changes in the net primary productivity of OP, changes of reductant input from the mantle to the surface, and net change in the size of the crustal organic carbon reservoir can all trigger a rapid transition from a low oxygen state to a high oxygen state. The tipping point is where the concentration of atmospheric O_2 is high enough for an ozone layer to form. Without an ozone layer the surface of the Earth and the atmosphere are exposed to UV radiation and this facilitates the reaction between atmospheric O_2 and methane. With the formation of an ozone layer, these reactions slow significantly and thus the concentration of oxygen can rapidly rise until a new steady state is reached with oxygen making up roughly 1% of the atmosphere within about one hundred thousand years (almost instant in geological timesales) (Lenton and Watson, 2011).

To reach this tipping point, O_2 levels must have been rising before the GOE. Hydrogen loss to space causes a steady, and irreversible oxidation of a planet (Hunten and Donahue, 1976). H can escape irreversibly from

Earth when CH_4 is decomposed in the upper atmosphere by ultraviolet light. The processes of photosynthesis and methanogenesis combined can be summarised by the reaction: $CO_2 + 2H_2O \rightarrow CH_4 + 2O_2$. This process is reversible as O_2 and CH_4 will readily react with one another in a short timescale of a few years. However with UV light decomposing the CH_4 we get $CH_4 + 2O_2 \rightarrow CO_2 + O_2 + 4H(\uparrow \text{space})$ where $(\uparrow \text{space})$ represents the H being lost to space. In this way, O_2 can build in the atmosphere (although prebiological atmospheric O_2 was limited to low levels (Kasting and Walker, 1981)). As methane makes up a small component of our atmosphere, the O_2 gained from this process today is negligible, however early earth is thought to have had an atmosphere far richer in CH_4 and so this process would have been more important for atmospheric O_2 levels at that time. A similar process does not happen with water vapour, as if H_2O molecules reach high altitudes they freeze and form clouds thus preventing them from reaching higher altitudes, this is known as the 'cold trap'.

Another cause of changing balance could be the decline in reduced material coming from the Earth's mantle. Over time, the Earth's internal heat source is reducing, as the radioactive isotopes decay. This means less energy to drive volcanoes and tectonic activity on the surface resulting in less input to the Earth's surface from the mantle. The material coming up from the mantle is highly reducing, meaning that it readily reacts with O_2 and thus removes it from the atmosphere. Over time this upwelling becomes less and thus less atmospheric O_2 is removed over time. The spread of OP could also potentially cause this shift although there is no direct evidence either way. OP could also lead to a net accumulation of organic carbon in the shallow sea shelves newly formed in the Archean, although no evidence has been found that directly points to this (Lenton and Watson, 2011).

After the Great Oxidation suddenly there was enough oxygen for aerobic respiration to become the dominant process of breaking down organic matter for energy in surface environments. This meant much more energy available to life and allowed cells to get larger, more complex, and to become more active. The ozone layer meant that life was now much more protected from the Sun's damaging ultraviolet rays and no longer needed defences against this, possibly reducing the difficulty of colonising the land. However, life that used oxygen in its metabolism and life that lived in the oxygen rich surface environment now had to develop a new set of defence mechanisms to protect itself from highly reactive oxygen. Life that did not evolve defence mechanisms was banished to sediments and the anoxic water of the deep

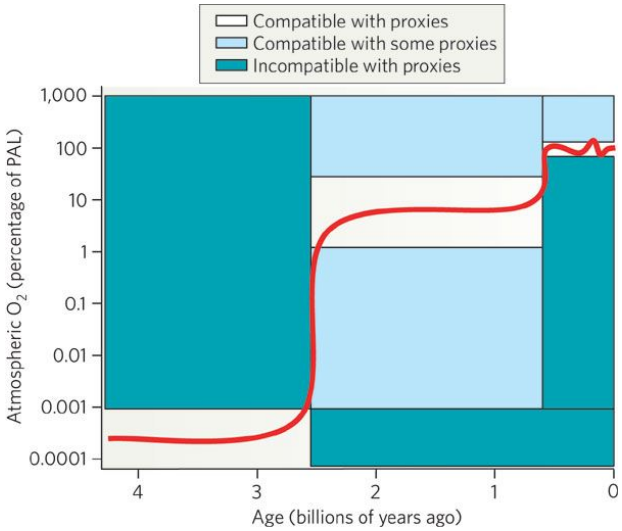
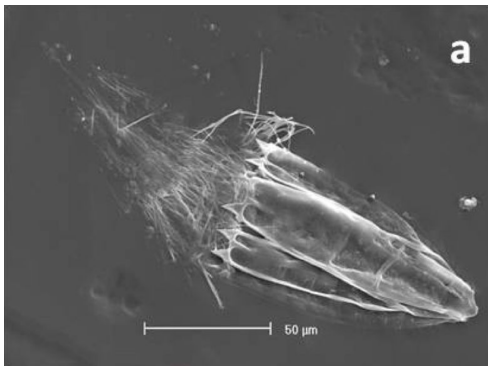


FIGURE 1.3: Red line shows the changing atmospheric oxygen concentration over time with respect to present day levels (PAL). Image from (Kump, 2008)

ocean.

Anaerobic life still inhabits sediments, animal guts, and other places with little to no dissolved oxygen. This life was thought to be limited to single celled organisms, however recently multicellular creatures have been found living their entire lifecycle in the deep hypersaline anoxic basins of the Mediterranean Sea (Danovaro et al., 2010). This is the first multicellular life confirmed that never requires oxygen at any part of its lifecycle, Figure 1.4a.

How oxygen levels rose to todays levels from the levels present after the GOE is less well understood. A second significant rise in atmospheric O_2 (Figure 1.3), known as the Neoproterozoic oxygenation event (NOE) (Och and Shields-Zhou, 2012), has been proposed to have occurred at roughly 575 Mya during which time the deep oceans became oxygenated (Canfield, Poulton, and Narbonne, 2007). This was followed by the appearance of animals, and then the Cambrian explosion around 50 million years later, and the NOE is thought to have been necessary to allow for both of these events to occur, as animals have certain oxygen requirements (Campbell and Squire, 2010), Figure 1.4b. The exact timings and cause of the NOE is less well constrained than for the GOE (Och and Shields-Zhou, 2012), and some propose that it did not occur at all as evidence for it is lacking, but that instead that the rise of plants around 400 Mya caused oxygen levels to reach modern day levels (Lenton et al., 2016). Whenever it occurred and whatever caused it, atmospheric oxygen levels rising to today's levels is what allowed us to appear on the scene many millions of years later.



(A) Electron image of the only multicellular life found to spend its whole life cycle in an anoxic environment. Image from (Danovaro et al., 2010).

(B) Example of complex life requiring oxygen to survive. This cat has defence mechanisms against the highly reactive O_2 that she requires to survive.

FIGURE 1.4

2 .3 Global glaciation events – Snowball Earths

The Snowball Earth hypothesis (Harland, 1964; Kirschvink, 1992) postulates a series of global glaciations in Earth's history, where the Earth's surface was entirely, or almost entirely frozen, with each 'Snowball Earth' lasting for millions of years and ending in very warm periods due to a build up of greenhouse gases (Schrag and Hoffman, 2001). Current evidence points to two historic snowball Earth events – the 'Sturtian' that began around 716 Mya and persisted until 660 Mya (Bowring et al., 2007; Macdonald et al., 2010; Lan et al., 2014; Rooney et al., 2014; Rooney et al., 2015), and the 'Marinoan' which is thought to have began around 640 Mya and ended at 635 Mya (Hoffmann et al., 2004; Calver et al., 2004; Condon et al., 2005; Prave et al., 2016). Each of these events is thought to have ended in very warm periods due to a build up of greenhouse gases (Schrag and Hoffman, 2001). The weaker Sun during this time is also thought to have contributed. Evidence for these events comes from deposits and features found in rocks that were at the equator at the time (determined by paleomagnetism) that are typical of glacial movements and deposits (Kirschvink, 1992; Hoffman et al., 1998). Moving ice carries finely ground rock, stones, and boulders that travel on the surface of the Earth and leave striations (scratches). Glaciers can also transport and drop rocks that form distinct layers which we can see millions of years later as indicators of past glacial presence.

As the continents have moved, collided, and broken up many times since these glaciation events we cannot use the location of present day rocks to determine where they were during a Snowball Earth. However the glacial

sediment laid down during a glaciers journey contains small grains of magnetic particles such as iron, which tend to align themselves with the Earth's magnetic field. We can measure this magnetism hundreds of millions of years later to calculate the direction of the magnetic field the particles aligned themselves with, and thus what latitude of the planet the rocks were when they were formed (Lenton and Watson, 2011).

A Snowball Earth state is entered via an ice-albedo runaway positive feedback loop which only happens when the ice cover reaches 30^oN/S. An initial perturbation cools the planet, which causes ice sheets to advance to lower latitudes. This increases the albedo of the planet, reflecting more sunlight back into space, and further cooling the planet. This encourages more ice in a positive feedback until the ice has reached the equator and the planet is completely encased in a frozen shell.

To push the planet into an ice-albedo runaway feedback loop to reach a Snowball Earth state requires an initial perturbation – a reduction in global temperatures large enough for the ice cover to reach the tropics (30^oN/S). Various mechanisms have been proposed as providing a perturbation for these snowball Earth events. For example, the continental break-up of Rodinia (around 750 Mya) will have brought previously very dry areas of land closer to the ocean, making them wetter and increasing weathering rates, thus rapidly decreasing atmospheric CO_2 levels and contributing to triggering a runaway glaciation (Hoffman, 1999; Donnadieu et al., 2004). Changes in biological activity, such as life colonising the land, have also been proposed as providing a Snowball Earth causing perturbation (Tziperman et al., 2011; Heckman et al., 2001). Life on previously uninhabited land would accelerate silicate weathering, removing more atmospheric CO_2 and lowering the temperature. Additionally carbon burial into decay resistant land plants would have further depleted CO_2 levels, further lowering global temperatures and increasing ice coverage at the poles possibly triggering a run away ice-albedo affect leading to a Snowball Earth.

The earliest known possible Snowball Earth event followed the Great Oxidation Event. The Huronian Glaciation Event is thought to have occurred globally from 2.29 Gya - 2.25 Gya (Tang and Chen, 2013), although it is debated as to whether this glaciation completely covered the Earth in ice, or whether glaciation occurred at different parts of the globe at slightly different times. As the newly abundant atmospheric oxygen reacted with the methane rich atmosphere at Earth in the time, it reduced the insulating properties of Earth's atmosphere causing widespread glaciation.

If the Earth did enter Snowball states in the past, it clearly exited them at some point as our world today is not frozen. The carbonate-silicate geochemical cycle is thought to have played an important role in our planet thawing from a Snowball Earth state. If the globe is covered in ice, plate tectonics will continue uninterrupted and the rate of volcanic eruptions pumping CO_2 into the atmosphere will be unaffected. Silicate weathering however – a chemical process that removes CO_2 from the atmosphere – will be dramatically reduced as it is moisture and temperature dependant. As the temperature increases, silicate weathering rates increase, and as the temperature decreases, silicate weathering decreases. Under normal conditions this provides a negative feedback loop that acts to stabilise global temperatures, as when the temperature rises, more insulating CO_2 gas is removed and as temperatures fall, less is removed. The timescales over which silicate weathering has an effect are of the order of a million years, much slower than the consequences of sea-ice-sheet growth which can take just a matter of months to have an impact. Thus, while the silicate cycle in unable to prevent a runaway ice-albedo affect if the planet is sufficiently perturbed, it does give a possible escape mechanism from a Snowball Earth (Hoffman et al., 1998). During a Snowball Earth event, with silicate weathering rates drastically reduced, but volcanic activity unaffected, CO_2 levels in the atmosphere would rise. This would allow temperatures to rise until the ice can start to melt. There would then be a runaway feedback of global warming as the ice melted, reflecting back less sunlight, further warming the planet and allowing further melting of ice. The planet would thus rapidly leave the Snowball Earth state.

The amount of CO_2 thought to be necessary to exit a Snowball state has caused some problems for the hypothesis. Early predictions based on models predicted that a partial CO_2 pressure of 0.12 bar would have been enough to trigger deglaciation from a Snowball Earth (Caldeira and Kasting, 1992). Later models including atmospheric dynamics excluded from earlier models found that even a partial CO_2 pressure of 0.2 bar (550 times the present day level) was unlikely to trigger deglaciation on a completely frozen Earth (Pierrehumbert, 2004; Pierrehumbert, 2005). Higher partial pressures of CO_2 resulted in unreliable results from the model.

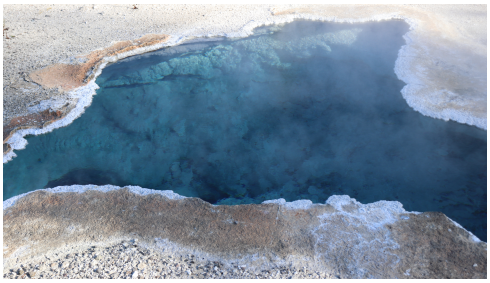
A potential solution proposed to the problem of exiting a Snowball Earth is ash deposited on the surface of the ice following a mega volcanic eruption, as this ash would reduce the albedo of the planet. Models (Le Hir et al., 2010) have shown that snow 'dirty' with ash might be a key factor for deglaciation, and that a 'dusty Snowball Earth' could reach the deglaciation threshold for

the CO_2 levels thought to be present at the time.

Criticisms of the hypothesis have focused on the implications of a globe covered in ice for biology. How could life survive extended periods of total ice coverage? For simple single-celled life, a hard snowball earth does not present much of a problem. Many bacteria can be frozen for long periods of time and survive (Christner et al., 2003; Dieser, Battista, and Christner, 2013). Many types of bacteria can produce an anti-freeze that prevents the bacteria from bursting as it freezes. Then when thawed some time later, the bacteria can go on as normal. Bacteria isolates have been successfully recovered from ice drilled from an icecap in Western China that is over 750,000 years old, demonstrating the durability of bacteria in ice (Christner et al., 2003).

For more complex eukaryotic life a hard snowball earth would provide more of a challenge, however as oxygen levels rose quickly after the end of the later snowball earth, this indicates that some eukaryotic life survived. Fossil evidence also exists for shelled amoeba persisting through later snowball earth events apparently unharmed (Bosak et al., 2011). At the equator the ice may have been thin enough for light to penetrate and allow photosynthesising organisms to survive (McKay, 2000), Figure 1.5a. Hot surface springs would have also produced warm lagoons, similar to the kind currently found in Iceland and Yellowstone for example, Figure 1.5b, providing oases for life in the cold desert. Hard snowball earth supporters suggest that hot springs, and cracks in the ice would provide 'safe-havens' where life could flourish through the millions of years the Earth was frozen (Lenton and Watson, 2011).

(A) Algae growing under the ice of Antarctica. Photo credit: Lars Chresten, Lund Hansen.



(B) Hot springs in Yellowstone national park. Photo credit: Elara. Nicholson.

FIGURE 1.5: Examples of possible havens for life during a Snowball Earth event. Image in (a) from (Høgslund and Bondo Christensen, 2015)

An alternative theory to a 'hard Snowball' is known as the 'Slushball Earth' hypothesis (Lewis, Weaver, and Eby, 2007). On a Slushball Earth, there would be wide-scale glaciation, but this glaciation would not fully reach the equator as is hypothesised for a Snowball Earth. In a Slushball, at the equator there would be a band of open, or at least seasonally open water, and this would remove the issues surrounding eukaryotic life surviving a full Snowball Earth. The Snowball vs Slushball debate is far from over, however there is compelling evidence that at points in history Earth may have been entirely frozen, and if this were the case, it is something that life on Earth, even complex life survived.

3 Summary

In this Chapter I have outlined a very quick introduction to the history of Earth, focusing on what the planet was like when the earliest life forms appeared, and on some of the large-scale changes that occurred on Earth since life emerged. The Earth life first appeared on is vastly different to the Earth today, and since the arrival of life, the planet has undergone many changes, some very rapid on geological timescales. These changes would have provided a challenge to life at the time. To put the timescales in this chapter into some sort of context, the earliest humans are thought to have evolved around 2 Mya (Alemseged, Coppens, and Geraads, 2002). We are very recent addition to Earth. Figure 1.6 shows a timeline of the key events covered in this chapter. All dates are exact and taken from the work referenced in this Chapter.

Figure 1.6 shows the eons that many of the events discussed in this Chapter occurred in. The Hadean eon begins with the formation of the Earth and ends when the late heavy bombardment may have occurred. The Archean starts where the Hadean ends, and far more rocks date from this eon than for the Hadean, the Archean ends when O_2 first appears in the atmosphere taking us into the Proterozoic which ends with the Cambrian explosion. The current eon is known as the Phanerozoic although some have suggested that with human caused climate change we are entering a new eon, the Anthropocene (Crutzen, 2006; Lewis and Maslin, 2015).

With such a dynamic history it seems remarkable that life has persisted uninterrupted for at least 3.5 billion years, and the dynamic past of Earth also raises questions for the possible futures of our planet. Have we been lucky to make it this far? Or is the maintenance of habitable conditions on Earth,

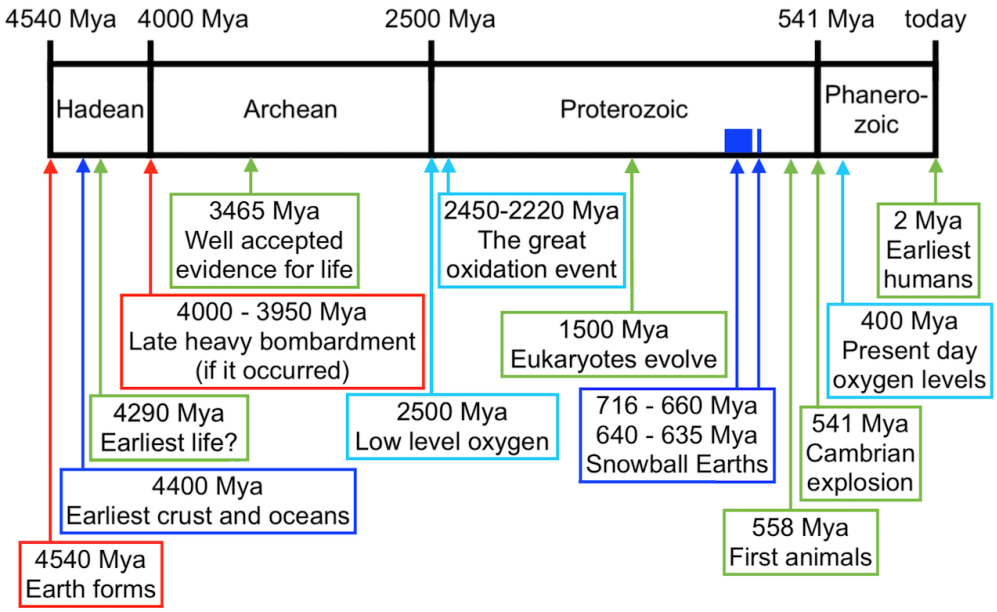


FIGURE 1.6: A timeline of the key events of Earth's history covered in this Chapter and the eon they occurred in. Timescale is in terms of millions of years ago (Mya). Scale of timeline is not exact. Dates complied from multiple sources, see main text for discussion and references.

despite large internal and external perturbations, to be expected of a planet harbouring life? In the next Chapter I introduce the Gaia Hypothesis – the central topic of this thesis – and how this hypothesis addresses how habitable surface conditions might be maintained on a planet facing, at times, extreme changes, both due to external and internal perturbations.

Chapter 2

Introducing Gaia

In this Chapter I introduce the Gaia hypothesis, covering its early conception and later development.

1 The Gaia Hypothesis

In the 1960's NASA set up its planetary exploration program with a mission to determine whether there was life on Mars. Scientist James Lovelock was hired to design life-detection experiments. By considering planets other than Earth, humanity was forced to view life on Earth from a new perspective. From space, the Earth is one self contained entity, with clear boundaries within which exists everything we know, our oceans, atmosphere, rocks and life, Figure 2.1. Many suggested life-detection experiments focused on finding organisms or by-products of life, and required sending robots to Mars. Lovelock realised however that a visit to Mars was not necessarily required to determine whether the planet hosted life. Lovelock recognised that the presence of life left fingerprints all over Earth, especially in the atmosphere (Schneider et al., 2013). The degree of chemical disequilibrium in our atmosphere is remarkable. We have an atmosphere rich in CH_4 and oxygen, a reactive mix, and yet the quantities of each have remained stable over geological time periods. Lovelock realised that life was a key player in maintaining this high level of atmospheric chemical disequilibrium, and that such a feature in the atmospheres of other planets could be used a 'bio-signature' – a marker for an inhabited world (Lovelock, 1965). Without life's influence, Earth's atmosphere would be drastically different to what it is today, see Figure 2.2. With this realisation, Lovelock determined that Mars, with its atmosphere (in contrast to Earth's) very close to chemical equilibrium, was almost certainly devoid of life. Lovelock, together with microbiologist Lynn Margulis, developed these realisations into the Gaia Hypothesis (Lovelock and Margulis, 1974; Margulis and Lovelock, 1974).

FIGURE 2.1: The Earth as seen from the Moon. Image taken on 24/12/1968 by Apollo 8 astronaut William Anders (Anders and NASA, 1968).

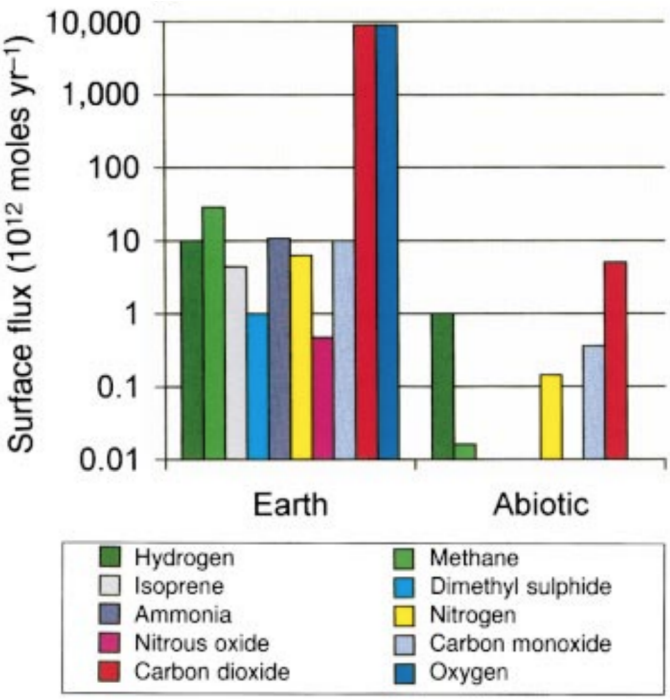


FIGURE 2.2: Comparing the atmospheric composition of an Earth without life (labeled Abiotic) and pre-industrial Earth with life. Image from (Lenton, 1998).

The Gaia Hypothesis (Lovelock and Margulis, 1974; Margulis and Lovelock, 1974) proposes that the Earth, with its biosphere, hydrosphere, lithosphere, and atmosphere, can be thought of as a single entity that self regulates within the narrow parameter limits that allow for life to survive and thrive; the whole Earth system – Gaia – can herself be thought of as somewhat like a living organism.

Life plays a part in regulating atmospheric CO_2 levels via a biotic rock weathering feedback (Watson and Lovelock, 1983; Schwartzman and Volk, 1991; Schwartzman and Volk, 1989) – in warmer times, life in the soil proliferates, breaking up rocks, and increasing the rates of weathering thus removing CO_2 from the atmosphere, which in turn causes a cooling of the climate, therefore via its impact on global CO_2 levels life impacts planetary temperatures. However, it is not just in the atmosphere that we see the fingerprint of life. All of the world's oceans have a nearly constant ratio of nitrogen to phosphorus, this ratio being a highly suitable ratio for life, and life is thought to play a role in water uptake to the Earth's mantle and thus impact the formation of plate tectonics (Höning et al., 2014).

Numerous books have been written by Lovelock on Gaia (Lovelock, 1979; Lovelock, 1988; Lovelock, 1991; Lovelock, 2007; Lovelock, 2009; Lovelock, 2015) exploring and expanding the hypothesis, and addressing the many criticisms the hypothesis attracted (see Section 2). As the hypothesis was developed, the definition of Gaia was tightened, moving away from language that could be considered teleological.

The Gaia hypothesis offers answers to the questions posed in Chapter 1. How has our planet maintained habitable conditions despite the increasing luminosity of the Sun and changing tectonic activity over geological timescales? How has life survived meteor impacts, huge volcanic events and Snowball Earths? Early versions of the Gaia hypothesis postulates that we would expect life to maintain its planet within habitable conditions, by bioengineering the atmosphere and hydrosphere to adapt to external perturbations, i.e. comet impacts or massive volcanic activity, and prevent these perturbations from rendering the planet unsuitable for life. In later versions of the hypothesis more emphasis is placed on the interplay between the biotic and abiotic components of the Earth, rather than life acting as a driving force. A Gaian planet would be characterised by a resistance to both internal and external perturbations (Lenton and van Oijen, 2002). While in short timescales dramatic global changes might occur, like the Snowball Earth events, it would be expected that over large timescales the planet would

return to conditions more suitable for life.

2 Criticisms of Gaia

When the Gaia hypothesis was proposed it was first ignored and then later vilified. Lovelock and Margulis both faced harsh criticism from the scientific community over Gaia. Partly this was due to the Gaia hypothesis appearing on the scene at a time when evolutionary biologists were focusing more and more on selection at the level of genes, and Richard Dawkins' book 'the Selfish Gene' had reached world wide success. The narrative had been moving in the direction of organisms acting purely selfishly for the propagation of themselves. Lovelock and Margulis were seen to be proposing the exact opposite, that all life on Earth worked together in harmony to ensure the long-term habitability of the planet.

The earliest criticisms were that Gaia implied teleology – that the hypothesis suggested life was aware in its impact on the planet and was actively striving to regulate it. Gaia was compared (Doolittle, 1981) to the fictional community on the moon created by the author Lofting (Lofting, 1975) where there is an absence of Darwinian competition and instead the animals and plants regulated life on the moon such that there was no war (however Doolittle now considers this criticism of Gaia to be wrong (Doolittle, 2019)). Some scientists, when Gaia was first proposed, did accept the large role life has played in altering our world, acknowledging an interdependence between life and the environment (Schneider and Londer, 1984), however they did not see life as a primary driver in the history of Earth. Geochemist Holland dismissed the Gaia hypothesis asserting of life's 3.8 billion year uninterrupted history: "I believe that this continuity is a consequence of the relative dullness of Earth history..." (Holland, 1984). The 'Daisyworld' model (Watson and Lovelock, 1983) was developed to address criticisms of teleology (see Chapter 1), and this model showed that global regulation can emerge in a coupled abiotic-abiotic system, with no conscious control by the biota required.

Further challenges to the hypothesis argued that any organism acting to improve the habitability of the planet would have to contend with "cheaters" who do not contribute and destabilise the system in the pursuit of their own interests (Dawkins, 1982; Szathmáry and Smith, 1995). To regulate its environment an organism presumably must play some role in maintaining the atmospheric composition and/or temperature on the surface of the planet

however any regulating effect would presumably come at some energetic cost to the organism. 'Cheaters' are species that do not contribute to the regulation but benefit from functions performed by other organisms. These non-regulating organisms would not have the cost associated with regulation and so could perhaps have a faster growth and reproduction rate due to being free of regulating responsibilities. These 'cheaters' could then outcompete the regulating species, thus destroying the regulating mechanisms and dooming the whole community. Critics asked how scenarios such as this could be avoided if the biosphere exhibits a strong regulating feedback on the planet. If life can have such a dramatic effect on the planet it would appear there are many more paths to self destruction than to self preservation. So why would a biosphere that interferes so strongly with the abiotic processes on our planet become self-regulating instead of self-destroying (Doolittle, 1981; Dawkins, 1982; Dawkins, 1986)?

The competitive edge of 'cheaters' is removed if the regulatory impacts of organisms is a by-product of their metabolisms (Volk, 1998; Lenton, 1998; Wilkinson, 1999). Models (see Chapter 2) have explored this scenario; an organism within these models still may not contribute to regulation while benefiting from the actions of others, however in these models there is no metabolic advantage for these cheaters. These criticisms were also addressed by Daisyworld variants and microbe models (Chapter 3). The Daisyworld model has often been argued to be an example of altruism – where an organism performs a function to benefit others, to the detriment of itself. This raises the question of how this sort of altruism might evolve (Hamilton, 1964). However daisies in Daisyworld are successful because they benefit themselves, not due to any 'good will' towards other daises, therefore altruism is not exhibited in Daisyworld. However because what benefits individual daises also benefits the daisyworld community, the model is a special case.

Another common complaint aimed at the Gaia is that is it is inconsistent with current understandings natural selection (Doolittle, 1981). Evolutionary biologists have argued that no mechanism for global regulation could be the result of Darwinian evolution as there are no 'competing' biospheres to allow for selection to take place. Therefore in the absence of competing biospheres, how could a self-regulating biosphere evolve? Mutation of genes is random and has no direction; mutations occur at some rate and the mutants either are unsuited to their environment and die, or are suited and live. These mutants can also change their environment, and natural selection provides evolution based on these random mutations at least the appearance of

some direction. The cumulation of these processes has resulted in a diverse array of species colonising every corner of the globe. This seems remarkable enough on its own. To then add that this biosphere also acts to directly regulate our planet's conditions and is the cause of the continued habitability of the planet seems perhaps to invoke the need for a conscious direction to evolution. An invisible hand insuring that biota which improved our planet's habitability were the ones to evolve and flourish and those that degraded it died out has appeared necessary to some if the Gaia hypothesis is correct.

Taking out the possibility of competing biospheres, which our solar system's history does not seem to allow for, one obvious answer to many of these criticisms would be that it is pure luck that our biosphere developed self regulation mechanisms, avoided self destruction or destabilisation from cheater species. After all we would not be here to ponder such questions had it not. This is known as the 'weak Anthropic Principle' (Carter, 1974; Carter, 1983) and certainly plays a role in answering these questions (Chapter 3 .5), however it is untestable, and a rather unsatisfying answer. Of course our past history must have allowed for intelligent complex life to emerge as here we are. But is that the whole story?

3 Which Gaia?

The Gaia hypothesis has been defined in numerous ways over the decades, and a taxonomy of these was suggested by Kirchner (1989), based on quotes on Gaia from papers and books by Lovelock and Margulis, as follows:

Coevolutionary Gaia Life influences its abiotic environment, and the environment in turn influences life.

Homeostatic Gaia Life influences the world in a way that leads to stability due to the dominant links between life and the abiotc world being negative feedback loops.

Geophysiological Gaia The biosphere can be described as a single organism, which can exhibit both homeostatic and unstable behaviour, like other organisms.

Optimising Gaia Life interacts with its physical environment in such a way that it maintains optimum conditions for life at all times.

'Co-evolutionary Gaia' is the only well accepted (Lenton, Schellnhuber, and Szathmáry, 2004) hypothesis. Free and Barton (2007) dismiss Geophysiological Gaia and Optimising Gaia as implausible, however deem Homeostatic Gaia as plausible but unproven. Homeostatic Gaia can be further broken down into two more hypotheses:

Lucky Gaia The Earth has homeostatic properties largely by luck (Watson, 2004).

Probable Gaia The probability for a life-planet coupled system to develop homeostatic properties is greater than the probability to evolve non-homeostatis (Lenton and Wilkinson, 2003).

Both these hypotheses agree that the abiotic-biotic coupled Earth system exhibits negative feedback cycles which have lead to the Earth having homeostatic properties. They also agree that that key global variables are maintained within habitable bounds by these processes, and that the Gaian system is resistant to both external and internal perturbations. The difference between the two, is that "Lucky Gaia" proposes that these feedbacks are in essence a coincidence, that there is no statistical likelihood for such negative feedback loops to have become dominant on Earth, that habitability-destroying feedbacks are more likely to occur, due to their number being greater (there are more ways to disorder something than to order it), and that we, on Earth are uncommonly lucky – Earth is highly atypical. "Probable Gaia" in contrast proposes that self-regulatory feedback loops are a statistically likely outcome on a planet with life. It poses that a Gaian system is an expected outcome on a planet where life emerges.

Lucky Gaia suggests that life in the universe is likely to be very rare, and that most planets which hosted life at any point in their history are highly likely to have had all life go extinct. Probable Gaia on the other hand suggests that life should not be such a rare occurrence in the universe. Assuming abundant planets with the conditions allowing for life to emerge, and that the emergence of life itself, given suitable conditions, isn't a highly unlikely event, we should expect alien life to be a common occurrence. There are a lot of assumptions at play there, and certain key ingredients would still be required to enable life to emerge at all, but once emerged, if life has a strong role in maintaining habitability on its host planet, then observer self-selection, while still certainly at work, plays a smaller role in explaining Earth's long term habitability.

Free and Barton (2007) argue that Optimising Gaia, and Geophysiological Gaia are implausible. Life has increased in biomass and diversity since its emergence and has colonised all corners of the Earth; wherever we look, we find something happily living there. This suggests that a weaker version of Optimising Gaia might be a viable hypothesis – that life will tend to improve habitability (but not optimise it). Ideas on 'perfect' conditions for life are difficult to define and there are many examples of lifeforms degrading their environment (e.g. biotic plunder (Tyrrell, 2004)) and so language such as 'optimal' perhaps clouds the more interesting question – can life not only maintain habitability but also improve habitability? While not the focus of this thesis, models suggest that this is indeed possible, see Chapter 2 .4.

Geophysiological Gaia seems to be a useful analogy for thinking about our living planet. 'Life' is ill defined – it's not clear what would constitute the first life on Earth. Viral particles are the most numerous biological entitles on our planet by far (Suttle, 2007), but are viruses alive? There are arguments in favour of viruses being classed as alive (Pearson, 2008), and arguments against (Moreira and López-García, 2009). There are also hypotheses that viruses were vital to the formation of certain mechanisms we associate with life, e.g. DNA replication (Forterre, 1999; Villarreal and DeFilippis, 2000; Forterre, 2002), or the development of cell walls (Jalasvuori and H., 2008). It's also unclear what constitutes a single life-form, or many (Clarke, 2010). A grove of aspen trees might look like a collection of separate trees yet they are all connected underground and all share resources via their shared root system (De Byle, 1964). So is an aspen grove a collection of individuals or a single entity?

With an exact definition of life being difficult to pin down (unsurprising as life must ultimately emerge from non-life), I see no real harm in extending the concept of a 'life-form' to scales on the planetary level. In any case, the Earth was never argued to be alive in the same way that I, a microbe, or a tree are alive, but to behave in a ways that can be compared to such life-forms as illustrated by the following quote:

> ... it dawned on me that life was regulating climate as well as chemistry. Suddenly the image of the Earth as a living organism able to regulate its temperature and chemistry at a comfortable steady state emerged in my mind. At such moments, there is no time or place for such niceties as the qualification of 'of course it is not alive – it merely behaves as if it were' (Lovelock, 2001)

Lovelock worked as a biochemist (amongst other things) leading to more emphasis on metabolism as a marker for life (which Earth can be thought to have with its various biogeochemical processes). For a molecular biologist genetics are seen as far more central to life (Wilkinson, 2006). If we were to class Gaia as a life-form it would clearly be a quite different one to a wolf say, but the wolf itself is made up of cells, which themselves contain mitochondria, the mitochondria cannot live outside the cell, nor can the cell survive outside the wolf. Why not then extend this to the wolf being unable to live outside Gaia? Understanding systems as a whole can provide insights that are clouded by reductionist thought processes. Just as functioning mitochondria are key for our health, wolves are key to the health of certain ecosystems such as that of Yellowstone National Park.

When wolves were eradicated from Yellowstone in the 1920s (Stahler, Smith, and Guernsey, 2006), the impacts were far reaching; the number of elk increased under reduced predation, and caused overgrazing. This contributed to the decline of aspen (Ripple and Larsen, 2000), and impacted the number of beavers surviving in Yellowstone due to the overgrazing of willow that beavers depend on for food and building material (Baker and Hill, 2003). This in turn impacted the hydrology of the park (Wolf, Cooper, and Hobbs, 2007). Since the reintroduction of wolves to Yellowstone in 1995 (Bangs, 1996; Phillips, Smith, and O'Neill, 1996), Aspen is recovering (Ripple and Beschta, 2007), and 4 beaver colonies have been established in the northern range of the park, where previously there were none (Smith, Peterson, and Houston, 2003). Beaver dams in turn increase the biodiversity of aquatic life (Collen and Gibson, 2000) while increased growth along riverbanks due to the decreased foraging by elk (Ripple and Beschta, 2006) provide habitats for birds and small mammals, and help stabilise river banks, reducing soil erosion (Beschta and Ripple, 2006). The presence of wolves also increased the carrion available for the many species that depend on this throughout the winter (Wilmers and Getz, 2005), such as ravens, eagles, and bears (Wilmers et al., 2003). All of this by reintroducing a key predator back into the ecosystem.

Yellowstone demonstrates that interfering with complex ecosystems and acting as if each part is separate can have far reaching consequences. Just as we require healthy organs to survive and thrive, Gaia requires healthy ecosystems. We cannot be pulled apart into our separate components and remain viable, and nor can we dissect Gaia and be surprised when the results are damaging to the planet. If we disrupt each part of Gaia by decimating her ecosystems, we harm our planet as a whole. It's well accepted that if you

FIGURE 2.3: Restoring wolves to Yellowstone National Park impacted the whole ecosystem. Image NPS/Jim Peaco (*Wolves*).

poison the wolf, it will likely die. Why then does the notion of poisoning the Earth face resistance? Geophysical Gaia is not the focus of this thesis however I feel that such language, inspiring people to view our Earth as a living system, and as a whole, can be useful, especially under the current global-scale human 'experiment' we are currently carrying out with climate change. It gives a perspective on our planet that is intuitive to humans (Lovelock, 2003) and I believe this holistic view of the Earth is needed.

4 Summary

In this Chapter I have provided a brief summary of the Gaia hypothesis including some of the variations of the hypothesis. It is now accepted that life has drastically altered the Earth and plays a role in regulating the chemical compositions of the atmosphere and ocean. Research is starting to show that life might even have impacted the development of plate tectonics on Earth (Höning et al., 2014). The real question to me is whether Gaia is 'lucky' or 'probable' – whether we are uncommonly fortunate on Earth, or whether a planet hosting life will have a tendency to develop self-regulatory feedback loops that help maintain conditions suitable for that life.

With only a single data point – Earth – it is hard to know how probable our current circumstances are. Models provide a way to investigate the mechanisms that might have lead to global regulation from the interaction of a biosphere with its abiotic world. We can observe what behaviours these coupled systems have, and how they are affected by external, and internal, perturbations and shocks, i.e. a slowly warming host star. These models can give us insights as to how our Earth system behaves and perhaps were we might be heading with our current global climate-altering actions, and it could give us an idea of what to expect in our search for life elsewhere in the

universe. There have been a number of models designed to test aspects of the Gaia theory. In the next Chapter I will give an overview of some of the key models in the literature and outline the criticisms of the Gaia theory they address, and the limiting assumptions of each model.

Chapter 3

Gaian Models

Much of the history of the Gaia hypothesis is linked to the development and exploration of Gaian models. These models were motivated by criticisms of the hypothesis and have shown how global regulation can emerge in systems without invoking any sort of conscious collaboration. Here I will give an overview of some of the key Gaian models to date, and the regulation and selection mechanisms that are demonstrated by these models.

1 The Daisyworld model

Daisyworld (Watson and Lovelock, 1983) was the first Gaian computer model. While not directly relevant to the work presented later in this thesis, Daisyworld, as the beginning of Gaian-systems modelling, is a key part of the history of the Gaia hypothesis, and variations of Daisyworld are still being developed.

On an inhabited planet we can think of the biota and their environment as two parts of a closely coupled system. Changes of one can affect the other, which may then affect the original perturbation. The feedback could be positive or negative. If positive the feedback will enhance the initial perturbation – e.g. the Earth entering or leaving a Snowball Earth state (see Chapter 2 .3), and if negative it will dampen it – e.g. the near stable oxygen levels in the Earth's atmosphere are regulated by negative feedback with fire acting as an upper bound to the level of atmospheric O_2 (Chapter 2 .2). As the Earth's biota and environment is an incredibly complex system, Daisyworld was developed as a simple coupled system that could be described by a few simple equations, allowing its behaviour to be understandable. Daisyworld was also created to address some of the criticisms against the Gaia theory, mainly that for a Gaian system to emerge, evolution must have a direction and 'know' what will lead to global stability. Since its conception, Daisyworld has been updated multiple times to address some of the limitations of

the original model, investigate other criticisms aimed at the Gaia theory, and to test ecological ideas. There is a huge amount of literature on variations of Daisyworld and a comprehensive review of the Daisyworld literature can be found in (Wood et al., 2008). In this section, I will go into some detail on the original Daisyworld, and then highlight a few of the many adaptations of this model.

1 .1 The Original Daisyworld

The original Daisyworld imagines a grey planet with negligible atmospheric greenhouse effects, inhabited only by two species of daisy – light daisies and dark daisies, referred to as 'white' and 'black' daisies respectively. Black daises are darker than the bare ground, and so reflect less incoming radiation with the effect of warming the local environment, and the white daisies reflect more radiation than bare ground and so cool their local environment. Daisyworld orbits a main sequence star like our own. Daisyworld starts initially devoid of life, however the 'seeds' for each daisy species are assumed to lie dormant 'waiting' for habitable conditions. Daisyworld is characterised by a few simple equations governing daisy growth, which is dependant on the local temperature. All daisies share a growth curve which is zero below 5^oC and above 40^oC at a maximum at 22.5^oC, see Figure 3.1. The growth of each species depends on this temperature dependant growth rate, the resources available on Daisyworld, and the death rate of daisies per unit time.

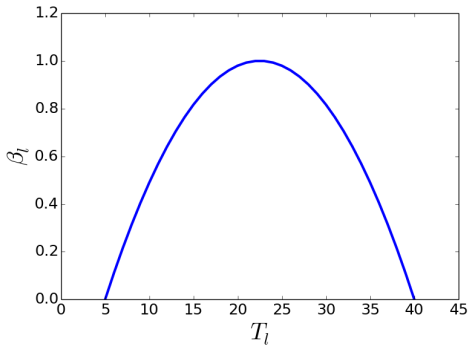


FIGURE 3.1: A plot showing the temperature dependant growth rate curve shared by both daisy species in the original Daisyworld model.

Each daisy on Daisyworld has a corresponding local environment which it impacts via changing the albedo of this locale. These local environments all interact with a global environment via diffusion. The original Daisyworld is

a zero-dimensional model. This means that the local environments on Daisyworld have no structure, i.e. daisies don't have nearest neighbours. All local environments only interact via a shared global environment. The impact of the local environment on the global environment is controlled by a parameter q that determines the diffusion rate between the local spaces in Daisyworld and the global environment. The global temperature of Daisyworld, T_g, is determined via equations balancing the absorbed solar radiation and the emitted radiation. A single global carrying capacity determines the maximum population of daisies that a planet can support.

White daisies cool their local environment with respect to the global environment, and black daisies warm theirs. Therefore on a cool planet, black daisies will have a selective advantage as they will boost their own habitability, and thus can spread, which will lead to the warming of the global environment and increasing the habitability of the world. The spread of black daisies will halt when their heating effect starts to negatively impact their habitability, i.e. they warm the world too much. On a warm planet, white daisies have the advantage and cool the planet as they spread, until their cooling impact becomes self limiting on their growth. The interplay of these two species leads to temperature regulation for a large range of incoming solar luminosity fluxes. This temperature regulation is due to the two negative feedback loops on daisy growth which are depicted in figure 3.2.

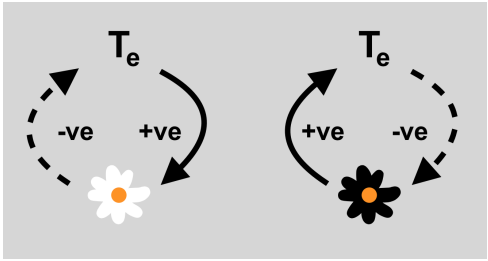
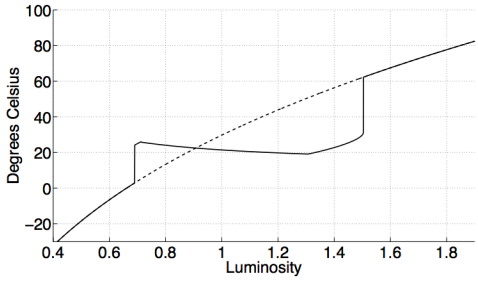


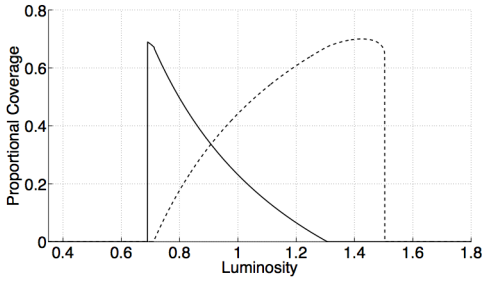
FIGURE 3.2: Figure depicting the two negative feedback loops that emerge in the original Daisyworld model. A solid arrow indicates that an increase in the source leads to an increase in the sink, i.e. an increase in the population of black daisies, leads to an increase in the global temperature. A dashed arrow indicates that an increase in the source leads to a decrease in the sink, e.g. an increase in the population of white daisies leads to a decrease in the temperature. Note that the sign of the feedback for each switches either side of the optimum growth T.

Daisyworld forms a system of non-linear multiple feedback loops with steady states where the number of black and white daisies changes to maintain a temperature close to the ideal growth temperature. For a large range

of T_g there are stable configurations of black and white daisies. In the Daisyworld experiments, the incoming solar radiation is slowly increased, mimicking the evolution of stars like our sun. As the incoming radiation changes, the Daisyworld system, if given sufficient time, responds to perturbations with the result of maintaining a near constant T_g. The changing incoming radiation impacts T_g which in turn affects the growth rate of each daisy species. In a warming world, white daisies will be more competitive as they act to cool their local environment. In this scenario, as the less well suited black daisies die off, and the better suited white daisies spread, the Daisyworld planet will be cooled by the increased albedo due to the increased coverage of white daisies. The growth of white daisies on a warming world will be self-limiting at the point where they begin to cool their planet past optimal conditions for themselves. In this way temperature regulation is maintained in Daisyworld. This scenario is laid out in Figure 3.3.



(A) Solar luminosity vs temperature.



(B) Solar luminosity vs daisy density. The dashed line represents white daisies, the solid line represents black daisies.

FIGURE 3.3: Plots showing daisyworld temperature (left figure) and density (right figure) of each daisy species, from (Dyke, 2010). We see that as the luminosity increases the temperature rises in a roughly linear fashion, but once the temperature is suitable for life, the temperature is kept near constant by the daises. At first black daisies appear and dominate in the cooler environment but as the luminosity increases the black daisies die off allowing for environment cooling white daisies to grow, until eventually only white daisies can survive. Eventually the luminosity is too high for white daisies to sufficiently cool the planet and all life dies off and the temperature regulation ceases.

Daisyworld is an example of 'niche construction' (see Section 3 .1) where daisies that improve their local environment have a selective advantage over those that do not, and so outcompete them, leading to global benefits as successful daisies' local environments interact with the global environment.

Daisyworld was the first Gaian model showing robust global regulation due the collective actions of individual agents, and multiple variants of the model have been explored. In the original paper Watson and Lovelock (1983) also explored what happened if the feedback mechanism was radically changed – keeping black daisies as warmer locally, but having them cool the planet instead of warm. This could be a scenario where warm temperatures cause water evaporation, leading to cloud coverage which ultimately cools the planet by increasing its albedo. In this case the black daisies outcompeted the white daisies and become the only species. As both species in this case cooled the global environment, but black daisies are locally warmer than while daises, the black daisies had a strong advantage and grew until they became self-limited, with an increase in daisy growth cooling the planet, pushing conditions away from the optimum and thus reducing the fitness of the black daisies. The subsequent decline in black daisy numbers would then cause a warming of the planet, leading to increased black daisy fitness. This again forms a negative feedback loop leading to temperature regulation.

1 .2 Spatial Daisyworlds

Each daisy in the original Daisyworld has its own local environment and this local environment contributes to a global environment via diffusion. There is no defined spatial structure; all local daisy environments interact in the same way with the global environment, and there is a single carrying capacity that determines the total population of the system. There is no notion of a 'location' of a daisy, nor do daisies have 'neighbours'. A 1D Daisyworld model (Adams and Carr, 2003) incorporates curvature based on a spherical planet (see Figure 3.4), with longitudinal strips grouped as global environments with a certain carrying capacity for daisies, and temperature diffusion occuring between the strips. This model exhibits stripe patterns, with stripes of pure black daises and pure white daisies instead of mixed groups. This is because for finite diffusion, stripe formation increases the heat transfer between the two regions. If a stripe of, for example, black daisies becomes too wide, the heat in the centre of the strip can become too hot causing the black daisies to die off thus providing an opportunity for white daisies to take over. Thus the maximum width of a stripe in this model is determined by the rate of heat transfer between longitudes.

2-D versions of Daisyworld have been developed where the planet is characterised by a grid (Von Bloh, Block, and Schellnhuber, 1997; Lenton and

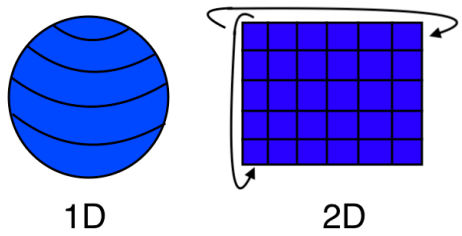
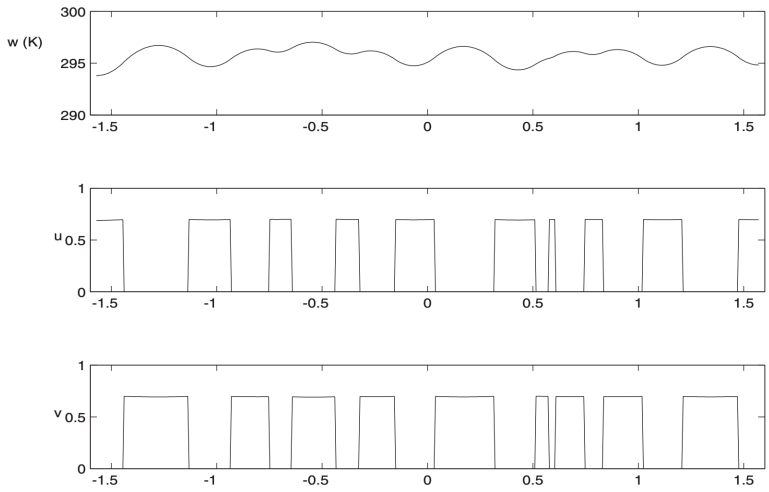


FIGURE 3.4: Diagram demonstrating how a planet can be represented in 1D or 2D. For 1D we have rings around the latitude of the planet in an approximation of a sphere. For 2D the surface is often represented as a grid with periodic boundary conditions, meaning that the far right connects to the far left, and the top connects to the bottom of the grid. This forms a doughnut shape. In both cases neighbouring sites interact via diffusion, instead of via a global shared environment as in the original Daisyworld.

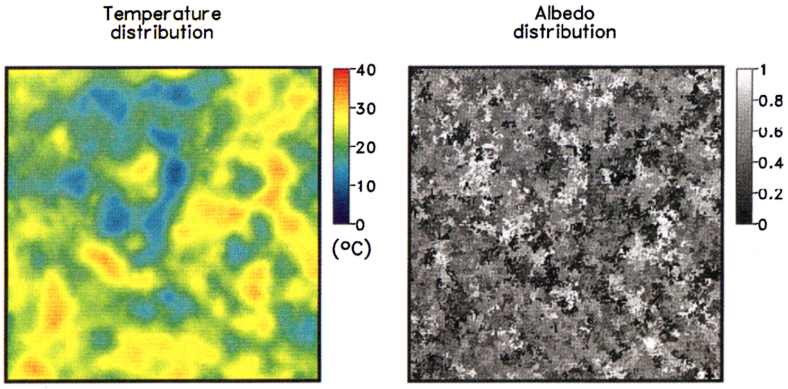
van Oijen, 2002; Ackland, Clark, and Lenton, 2003). These grids then have periodic boundary conditions, a simplification on the spherical shape of real planets (see Figure 3.4). Each grid point can be occupied or unoccupied at any point in time. Daisies die with a constant probability and unoccupied grid points can regrow daisies depending on the local temperature. The version presented in Lenton and van Oijen (2002) has the regrowth of daisies dependent on the daisy species in the neighbouring grid points. For example an empty grid point surrounded by only white daisies, could only grow a white daisy. Von Bloh, Block, and Schellnhuber (1997) take this further with mutation occurring with a constant probability during a seeding event. These mutations, if they occur, impact the new daisies' albedo, so that it will differ from its parent. Thus a continuous spectrum of albedos (between 0 and 1) are possible in this model. In this version with mutation, temperature regulation is almost perfect for a large range of incoming solar radiation values (Von Bloh, Block, and Schellnhuber, 1997; Ackland, Clark, and Lenton, 2003).

Figure 3.5 shows a the Daisyworld system in a temperature regulated regime for a typical run of the 1-D daisyworld model outlined in (Adams and Carr, 2003) and the same for the 2-D model presented in Von Bloh, Block, and Schellnhuber (1997).

Models with curvature in 2D have been studied (Ackland, Clark, and Lenton, 2003) and the curvature introduces inhomogeneous isolation of



(A) The 1D Daisyworld model (Adams and Carr, 2003) at equilibrium. K represents the temperature in Kelvin, u the population of white daisies, and v the population of black daisies, all for a given latitude.



(B) Figures showing the 2D daisyworld model (Von Bloh, Block, and Schellnhuber, 1997) at equilibrium, showing both the temperature distribution and the albedo distribution over the grid.

FIGURE 3.5: These figures show snapshots of the 1D (a) and 2D (b) Daisyworld models taken at a time when the systems are exhibiting stable temperature regulation. Images from (Adams and Carr, 2003) and (Von Bloh, Block, and Schellnhuber, 1997) respectively.

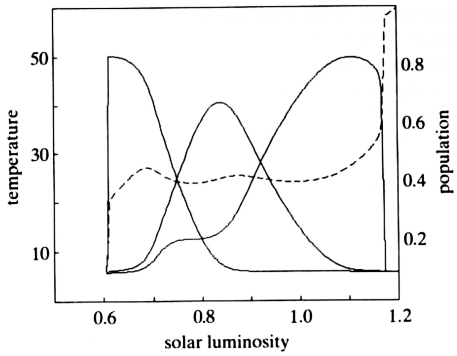
daisies that leads to the formation of deserts. As the isolation of daisies increases, the desert increases, with isolated bands of daisies unable to maintain habitable conditions at their locations. The increasing cover of desert causes the system to become unstable. Once the regulation from the daises both sides of the equator become insufficient, desert is formed at the equator. Before the desert forms a band around the equator of the planet, desert regions of roughly circular shape grow and shrink, until one fluctuates to a large enough size and expands, in a runaway positive feedback loop, to cover the whole planet. During this critical time, a small amount of cooling from daisies can prevent full desert formation, however once all of Daisyworld is covered in desert, the cooling needed to remove it is much greater.

1 .3 Evolution in Daisyworld

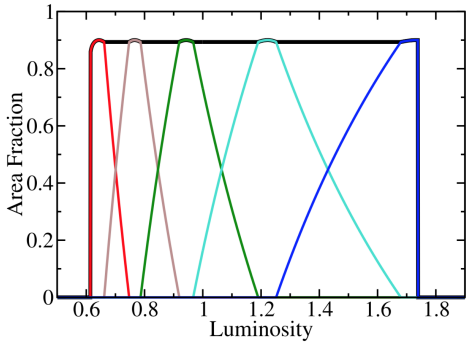
In the original Daisyworld there are two fixed species of daisies and no mutation takes place in the model. The system is always limited to just two phenotypes – black and white daisies, and this limitation determines the solutions to the Daisyworld equations. As cool daises can survive in warmer conditions and create a cooler climate, and black daisies act in the reverse, the model attracted criticism suggesting that the species in daisy world were chosen to have the correct regulation properties. Evolutionary biologists posed the question: how could such a self regulating system evolve via natural selection?

Dawkins (1982) first argued that a grey species of daisy could evolve that would “cheat” by benefiting from the climate regulation caused by the white and black daisies, while saving the energy of producing a pigment to contribute to this regulation, thus being more energy efficient and outcompeting the black and white daisies, leading to a breakdown in regulation. To address this, variations on the original Daisyworld were developed that included multiple daisy species, the first by Lovelock (1992), who included a grey “cheater" daisy, that had a faster growth rate due to not losing energy producing either while pigment or black pigment. This model showed that although grey daisies flourished when the temperature was ideal, they did not destabilise the regulation, and when the temperature was far from optimal they died off. When the grey daisies are abundant, the Daisyworld shows diminished strength of temperature regulation, however later work that included grey daisies but removed their faster growth rate (Lansing, Kremer, and Smuts, 1998), demonstrated that this was not due to the faster

growth rate of the grey daisies, but due to the presence of a third intermediate daisy species, see Figure 3.6a. Daisyworld was further expanded in Lovelock (1992) to include 5 daisy species, again each with differing albedos. Again, robust temperature regulation emerges from the 5 daisy model and it was found that when there were multiple different daisy variants only two types survived for any give applied temperature, see Figure 3.6b



(A) Graph of the temperature, and populations over time for each of the 3 daisy species when a third grey 'cheater' daisy is included in the model. Image from (Lovelock, 1992).

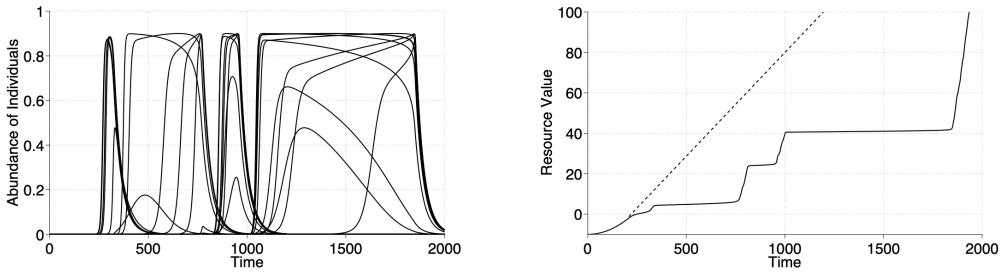


(B) Graph showing the populations of the different species when 5 daisy variants are included in the Daisyworld model. Image from (Wood et al., 2008).

FIGURE 3.6: Figures showing the behaviour of the model with more daisy species included.

The Daisystat model (Dyke, 2010) is yet another Daisyworld variant. In Daisystat, local space is removed and so all daisies share only a single global environment. This removes the ability of daisies to selectively improve their own environment and thus removes the mechanism that explains regulation in the original Daisyworld model. In Daisystat a large number of phenotypes of daisy are possible, and species no longer all share a universal 'ideal' environment, i.e. the growth curves of different daisy species will peak for different environmental configurations. The simplest version of Daisystat model has a single resource, which again could represent a temperature. This temperature, as in the original models is slowly increased over time. Daisies begin to grow when the temperature reaches a value that is suitable for them. The daisies suited to cooler environments will begin to grow first. As in the Daisyworld mode, temperature regulation is exhibited by the Daisystat model (Figure 3.7), but the mechanism behind this regulation differs. Now, the temperature is regulated by a mechanism called 'rein-control'. Rein-control is characterised by an environmental variable being 'pulled' in two different directions.

As the temperature rises in the Daisystat model, daisies will start to grow when conditions becomes suitable for them. Quickly two sub-communities of daisies emerge, those acting to warm the environment while preferring it to be cooler, and those acting to cool the environment, while preferring it warmer. Both thus form negative feedback loops where the increase of either sub-group is self-limiting as they begin to degrade their environment. The temperature that the system regulates at will be between the 'ideal' temperature of the two subgroups. As in the original daisyworld model, the Daisystat world is slowly warmed. The system moves from different regulated temperatures as the daisy community shifts in response to the forcing, shifting to regulating the temperature at higher temperature as the forcing increases. Due to the carrying capacity of the Daisystat, as the incoming temperature increases eventually a community will be unable to maintain the temperature at their regulatory temperature as not enough individuals are possible for substantial enough cooling and so that community dies out and another, preferring a higher temperature, takes over and regulation via rein-control is maintained at this new temperature. See Figure 3.7.



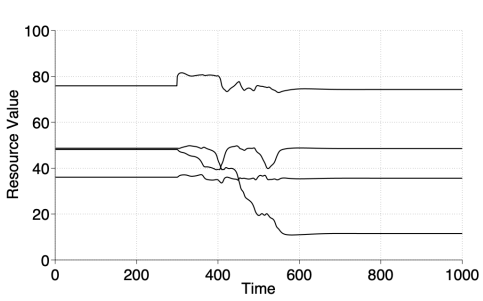
(A) The abundance of of the various daisy species over time.

(B) Resource value over time with the value (dashed) it would have in the absence of life.

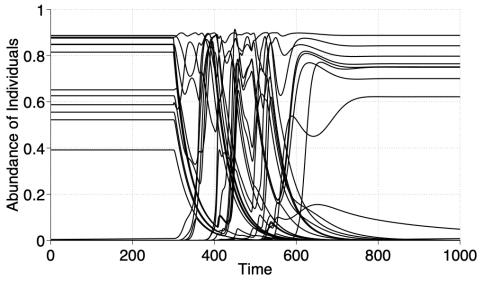
FIGURE 3.7: The abundance of the various daisy species over time. Periods of more gradual change in abundance are interspersed with rapid periods of large-scale change, where the daisy community undergoes dramatic changes before finding a new quasi-stable regime. Images from (Dyke, 2010).

The Daisystat has also been explored where the system must regulate 4 resources with daisy species all having different 'ideal' levels for these resources. The Daisystat system then exhibits interesting dynamics – regulation of all 4 resources robustly emerges, and the system exhibits homeostat

type behaviours where the system responds to shocks in the system by reconfiguring the daisy community until a new stable state is found. 'Ultra-stability' (Ashby, 1960) refers to the ability of a system to reconfigure its internal structure in response to perturbations that pull the system away from the 'desired' behaviour, in order to reinstate this behaviour. For example in the Daisystat, the desired behaviour is a stable value for each resource that supports a living daisy community. Figures 3.8 show this behaviour.



(A) Resource values over time.



(B) The abundance of daisy species over time.

FIGURE 3.8: Graphs showing the 4 resource values over time and the abundance of the various daisy species over time for an experiment where a perturbation was applied at time $t = 300$. This perturbation causes a period of rapid change until a new stable regime is found. Images from (Dyke, 2010).

Figure 3.8a shows the resource levels in a Daisystat system with 4 resources, over time. At around time $t = 300$, the system is perturbed causing a period of ongoing change until a new stable configuration of resource levels is found at around time ≈ 600. Figure 3.8b shows the populations of different daisy species over time for the same experiment as in Figure 3.8a. The stable configuration of the daisy community and the resource levels differ before and after the perturbation but the desired behaviour of a life supporting stable Daisystat environment is maintained.

2 Microbe models

Microbial models have been developed to investigate similar questions to Daisyworld – how and when regulation can emerge – but for more realistic scenarios. For most of the Earth's history all life has been microbial and so these microbial models are applicable to a large majority of the time life has existed on Earth. The models typically feature microbes with simple metabolisms that consist of a genetically determined food source, waste

product, and in some cases a by-product impact on certain abiotic parameters, e.g. pH, temperature, etc. The work in this thesis is based heavily on some of these microbe models and I will give a short overview of the models that are most relevant to the work presented in this thesis.

2 .1 The Guild model

The Guild model (Downing and Zvirinsky, 1999), is a microbial model that was developed to address the perceived problem of Gaia being compatible with natural selection. In a paper entitled "The Simulated Evolution of Biochemical Guilds: Reconciling Gaia Theory and Natural Selection" the authors show that the Guild model exhibits the emergence of a diverse community of interacting species whose combined impact on their global environment can result in the regulation of parameters such as temperature (Downing, 2000). The Guild model expands on the daisyworld models by including a larger range of diverse genotypes, and by incorporating nutrient recycling into the model, a feature not present in Daisyworld.

The Guild model is a simple abstract model of chemistry, biological growth and natural selection. It consists of a simple global environment with an inflow and outflow of 4 types of nutrients that can be used as food sources. Within this environment, each microbe interacts with its local environment via its metabolism, and then this local environment exchanges medium (this medium assumed to be a liquid) with the shared global environment via diffusion, see Figure 3.9. The fitness of a microbe is determined by how closely the nutrient ratios in its local environment match the genetically encoded 'ideal' ratios for the species the microbe belongs to. A real world example of this would be the the N:P ratio of the oceans that are regulated by life. These fitness ratios are identical for all species in the Guild model however metabolisms for each species are not. A microbe will eat nutrients in a certain ratio, and then excrete waste in the form of nutrients, with no species excreting what it consumes. The initial chemical ratios in the inflow differ from the preferred ratios of the microbes and initially this limits microbe reproduction and the total population remains low. Once near ideal chemical ratios are established they are maintained via the metabolisms of the microbe community.

In the Guild model nutrient cycling networks appear, as does regulation of global chemical ratios. As time progresses in the model, the ratios of nutrients in the global environment shift from the pre-set incoming ratios to

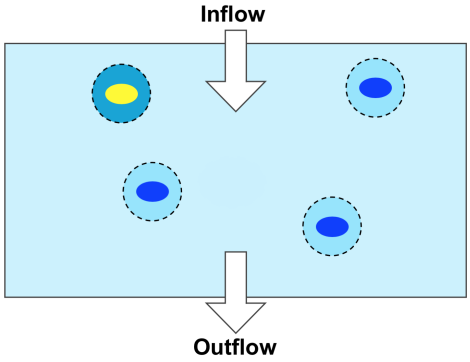


FIGURE 3.9: Diagram representing the Guild model environment. The environment has an inflow and outflow of nutrients to the global environment. Microbes are then represented as coloured ovals with different colours representing different species. Each microbe has a localised environment that it interacts with via its metabolism – removing nutrients via consumption and adding others via excretion. These local environments are semi-permiable and exchange nutrients with the global environment based on the relative concentration of each nutrient. As species have different metabolisms, the local environments of microbes belonging to different species will differ, represented in the diagram via the shade of blue of the local environment.

those closer to the maximum fitness of the microbes. This regulation is the net result of each microbe's metabolism. Microbes that cause their local environment to become more suited for life will reproduce faster than those who have a less positive, or even a negative influence on the habitability of their local space, and so these 'good' microbes will increase in number. The benefits these microbes then provide for themselves leak out into the global environment and thus can benefit other individuals of different species.

As in daisyworld, the organisms in the Guild model form a local buffer separating themselves from the global environment, enabling them to affect their own environment to a greater extent than other organisms' local environments. Unlike daisyworld however there are a huge number of possible species, determined by their genome

2 .2 The Flask model

The Flask model forms the basis of the new models presented in this thesis. A detailed description of a Flask model variant is contained in Chapter 4. Here I will give a brief overview of the original Flask models, without going into extensive detail, to avoid repetition.

The Flask model (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010) is characterised by an environment hosting simple microbes. For the Flask model version most relevant to this thesis, these microbes have a metabolism, consuming and excreting nutrients in set ratios as determined by their genetic code, and these microbes impact their abiotic environment as a by-product of their biomass creation. This by-product takes the form of adding a set value, between -1 and +1 to some abiotic parameter, which could be temperature, pH, salinity etc. This abiotic parameter in turn impacts the microbes' ability to consume nutrients and thus survive, depending on the microbes' environmental sensitivity.

In most variants of the model, flasks are connected in a ring structure, so that each flask has two neighbours and medium exchange takes place between each pair of neighbouring flasks. In this way, what the microbe community is doing in one flask can have impacts on others. During exchange between flasks, microbes too can be exchanged. Thus if some flasks have environment degrading communities, they will host a low population and be unlikely to spread this community to neighbouring flasks, conversely, flasks hosting a community that improves the flask environment will likely have a higher population of microbes and thus these microbes will be more likely to be moved to neighbouring flasks. In this way environment-improving microbe colonies can colonise empty flasks, and those hosting low numbers of microbes.

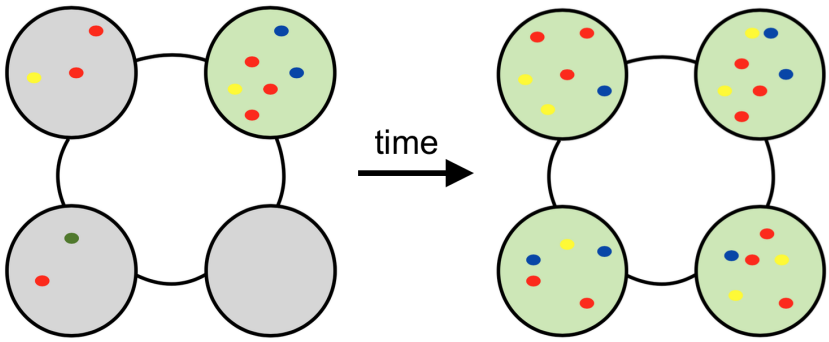


FIGURE 3.10: Diagram demonstrating higher selection taking place upon a series of flasks each hosting a microbe community. Green flasks indicate flasks hosting a microbe community that acts to improve its environment, and thus is able to flourish. Grey flasks lack this. After some time, communities that are successful in improving their flask environment will tend to spread to colonise other flasks during medium exchange between flasks (represented by solid black lines connecting flasks).

The Flask model removed the limiting assumption of Daisyworld and the Guild model that traits selected for at the individual level always improve the global environment. Instead as Flask model microbes affect the abiotic environment as a byproduct of their metabolism, these effects are selectively neutral at the individual level. The removal of this assumption does not prevent stabilising environmental regulation from emerging.

The first Flask model (Williams and Lenton, 2007), like the Guild model, focused on nutrient ratios and nutrient recycling. It found that within a single flask, where microbes have no local environment and only share a global one, that nutrient recycling emerged robustly and that nutrient ratios close to ideal for the microbe community present in the system could be found and maintained. Later versions of the Flask model (Williams and Lenton, 2008; Williams and Lenton, 2010) moved to multi-flask environments, and focused on an abiotic parameter that affected the microbes' ability to consume nutrients. As in Daisyworld, the microbes' fitness peaked when the environmental abiotic parameter matched their 'ideal' parameter value. This parameter can be thought of as a temperature, pH or salinity for example. The model in Williams and Lenton (2008) had all microbes sharing the same growth function, and the model in Williams and Lenton (2010) allowed different preferred conditions to evolve. In both these models, well mixed flasks containing microbes were connected in a ring. In each flask, all microbes shared a global environment, and no microbe had a local environment. There was flow between flasks that allowed some microbes to be transported from one to another. In both versions of the model, regulation of the abiotic parameter emerged.

The mechanism giving rise to regulation in the Flask model was argued to be a limited higher-level selection. In a connected environment, locations where local communities improve their environment achieve larger populations and thus can colonise and outcompete communities that degrade their environment leading to the spread of environment improving communities and thus global regulation.

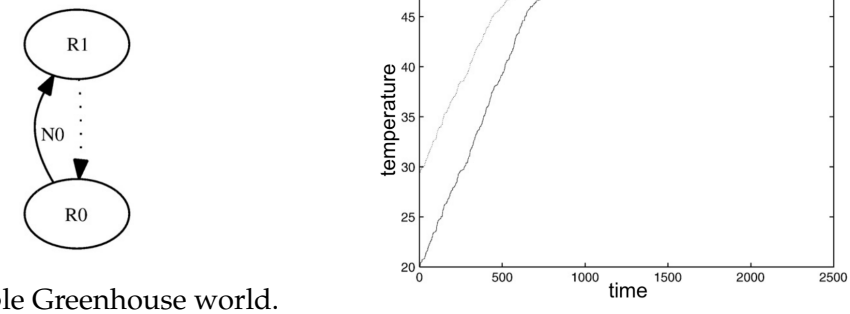
2 .3 Greenhouse World

Greenhouse World (Worden, 2010; Worden and Levin, 2011) is a model of an atmosphere represented by a network of compounds that can be transformed into one another as a simplification of real-world chemistry. These transformations can take place spontaneously via simple abiotic chemical reactions,

or via biological activities i.e. lifeforms consuming one compound and excreting another. The composition of the Greenhouse world atmosphere determines its temperature. Each species of microbe has an optimal temperature where its fitness is maximum, and it can only survive a few degrees either side of this optimum. There is only a global environment and so the whole community experiences the same environment at all times, however different individuals might be better suited than others for a particular environment, i.e. having an abundant food source and a habitable temperature. Mutation occurs in the model only when the Greenhouse system is in a stable state – e.g. the temperature is stable for significant timespans. In a steady system, a single mutation is introduced by taking one of the current members of the community and replicating it identically apart from a slight change, either positive or negative, to its optimal temperature. The experiment then continues with this new mutant. These mutations allow the Greenhouse community to adapt in small steps towards the current temperature of the system. Of course these mutations will then impact the balance of compounds in the atmosphere, in turn impacting the temperature and potentially leading to a shift in the relative populations of the species making up the community in order to maintain habitability.

Greenhouse world is explored both in a highly simplified case, and in a more complex scenario. The simplest version of Greenhouse world consists of just two resources R_0 and R_1 with a single abiotic reaction taking place $R_1 \rightarrow R_0$. R_1 is a greenhouse gas and thus has a warming impact on the world, whereas R_0 does not, so in a purely abiotic scenario, all R_1 would decay to R_0 and the planet's temperature would decrease to 0. Added to this is a single species N_0 which consumes R_0 and excretes R_1. N_0 has an ideal temperature of $T = 20$ and can only survive temperatures $T = 20 \pm 10$. Initially the stable temperature of the system is close enough to the preferred temperature of the Greenhouse world community for life to survive, but far from optimum conditions. Mutations bring the preferred temperature of microbes closer to the temperature of the system, but in turn impact the temperature of the system raising it further. Eventually over time, as more mutations occur the distance between the microbes' ideal temperature, and the temperature of the system converges. Figure 3.11 shows this simple Greenhouse world setup, and the evolution of the ideal temperature, and the system temperature over time.

A more complex version of Greenhouse world is also explored in (Worden, 2010) where a randomly generated network of chemical compounds and



(A) Simple Greenhouse world.

(B) Temperature over time.

FIGURE 3.11: Figures from (Worden, 2010) showing (a) the simplest Greenhouse world set up, with a single species (N_0) and two chemical compounds R_1 and R_0. Figure (b) shows the temperature of the system with a dotted line, and the optimal temperature of the microbes as a solid line. Over time, as mutations take place, these two temperatures converge.

microbe species is created. Such communities are rarely viable. Rather than going extinct, these systems tend to go through a period of climactic fluctuations and extinction events until a stable configuration is reached, which will consist of fewer species than the original setup. This process where unstable community structures give way until a stable configuration is found, in a series of restructuring events, is known as “sequential selection" (Lenton, Caldeira, and Szathmáry, 2004; Lenton, 2004; Betts and Lenton, 2007). From a complex randomly generated (typically) unviable community, the Greenhouse world models show that regulation can robustly emerge via sequential selection.

2 .4 The Tangled Nature model

The Tangled Nature model (TNM) is an ecosystem model of co-evolution (Christensen et al., 2002; Anderson and Jensen, 2005; Lawson, Jensen, and Kaneko, 2006; Laird and Jensen, 2006; Laird and Jensen, 2007). While this model was not designed to explore the Gaia hypothesis, it has recently been extended to include Gaian features (Arthur and Nicholson, 2017). The TNM consists of a 1D world that has a carrying capacity for life. Each simulation begins with a single species and mutations occur with a constant probability per reproduction event thus allowing for the appearance of new species. Species can impact one another’s growth rates either positively or negatively and these inter-species effects are not necessarily symmetrical. Species A

might experience an increase in its growth rate from species B, whereas species B might suffer from an increase in species A for example.

The model is characterised by periods of stability known as quasi-Evolutionary Stable States (qESS) where a stable population of dominant species (known as the 'core' species) co-exist for significant periods of time. These species will overall all positively impact one another's growth rates which is what leads to stability. Mutants frequently appear during qESS however most will not flourish as they will lack positive (or positive enough) inter-species interactions with the presently dominating species. However should a mutant appear that finds the current environment favourable, it can rapidly grow in number and disrupt the core. This can trigger what is known as a 'quake' – a period of rapid ecosystem reconfiguration where species go extinct and new species appear creating a new qESS. In the TNM, on average, the length of the qESS periods become longer and the chance of quakes occurring decreases as the system increasingly finds more and more stable ecosystem configurations that are less prone to perturbations. At the same time the diversity of the core species tends to increase over time, as does the total population of the ecosystem. Thus over time the TNM exhibits a behaviour of increasing stability coupled with increasing complexity.

After the collapse of a qESS the TNM world is sparsely populated by remnants of the old core and their nearby mutants (i.e. one mutation away from a core species) and the new 'core' will be formed from these species. The new core is likely to be the group of species that have the largest sum of mutually positive inter-species interactions, and given more potential species to choose from, over time the core tends to slowly increase in size as larger groups of species can have higher sums. There are also more possible species configurations involving a number of species than there are for those involving just 1 or 2 core species. The total population of the system also increases over time for similar reasons, with a larger pool of species to select from, there is more competition amongst species to establish themselves, and so those with more strongly positive interactions with one another, and so faster growth rates will become more dominant leading to higher populations on average over time.

Larger populations mean that there are more possible mutants that could potentially destabilise the core yet over time quakes become less likely in the TNM. As the inter-species interactions of the core members become stronger over time, any mutant will also need a stronger positive overall interaction with core members to destabilise the system, which becomes less likely.

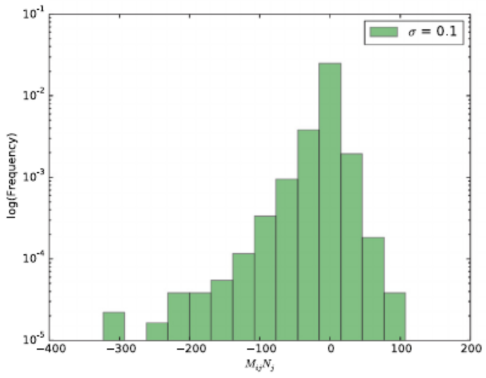
Therefore the system on average will have to wait for longer and longer time periods for a destabilising mutant to emerge.

The Gaian variant of the TNM (Arthur and Nicholson, 2017) involves species also affecting the abiotic carrying capacity. Instead of a constant carrying capacity as in the original TNM the carrying capacity becomes a function of the type and population of the species present at any time. In this extended TNM model there are three terms which contribute to the fitness of a species A:

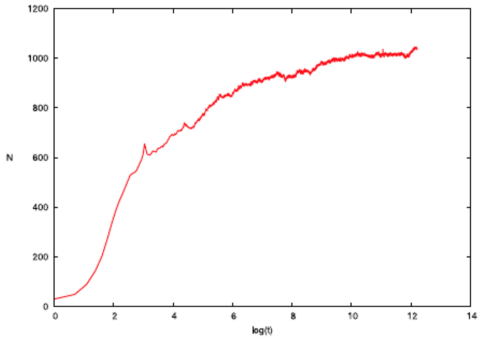
- direct impacts of species B on A e.g. species B eats species A
- the physical effect species B has on the environment of species A, e.g. B nests in the same sites as A
- the interaction between A and B whose strength is proportional to the population of B, e.g. the byproducts of species B impacts species A's ability to reproduce.

As the population of various species change, their impact on other species due to the summation of their impact directly on the species, and on the shared environment, can change. It can go from positive to negative, negative to positive, become more positive, or become more negative. An example of an increase in a species causing an initially positive interaction with another species to become negative would be algae in a lake – in small numbers they provide food for fish, but an algae bloom can cause the death of the very same fish. With this setup this TNM version is directly able to address the criticism of Gaia of "cheaters" – species in the TNM are possible which benefit from an environment while not contributing or even degrading the environment.

On average the results of this model find that although species destroying the system's habitability do occur, and such species trigger 'quakes' in the system, the system tends to recover on average with a more complex and more stable eco-system emerging out of the chaos of the last quake. In the vacuum left after a quake, species with faster growth rates are more likely to form a part of the new core and this over time will lead to an average increase in population size. As with the original TNM, over time, due to increasing competition for resources with larger and larger cores, mutant species find it harder to become established, leading to fewer ecosystem collapses over time.



(A) Histogram of species-environment interaction values.



(B) Graph showing the average total population over time for TNM systems.

FIGURE 3.12: Figures from Arthur and Nicholson (2017). (a) Shows a histogram of the species-environment interactions of all species alive at any point in an experiment for 1000 experiments. Notably this histogram is not symmetrical, there are more environment improving (negative values) species than there are environment degrading. Figure (b) shows the total population over time averaged for 1000 experiments. We see a general trend of increasing population. Note the log(x) axis.

In a sparsely populated system, the species' inter-species interactions are more important than each species impact on the environment – a single agent degrading the environment does not have much impact. Therefore environment degrading ecosystems can emerge. These ecosystems however will be more prone to collapse as they will host a smaller population, making it more likely for mutants to destabilise the system. Environment improving ecosystems will enjoy larger populations, and thus be at a lower risk of quakes. This means that over time there is a larger probability of finding an environment improving ecosystem over a degrading one.

3 Key Regulation and Selection Mechanisms

I will now give a brief summary of the key regulation mechanisms responsible for maintaining habitable conditions in Gaian models, and the selection mechanisms for systems exhibiting regulatory behaviours.

3 .1 Niche construction

Niche construction is the process whereby organisms via their activities, for example their metabolic processes, or the building of a structure (e.g. a spiders web or a badger sett, Figures 3.13), in part both create and destroy their

own niches (Odling-Smee, Laland, and Feldman, 1996). Therefore organisms not only adapt to their environment but they also play a part in creating it (Bendall, 1983). Selection can then take place on organisms, with those contributing to a better environment for themselves, and thus boosting their own fitness tending to spread, while those that degrade their own environment becoming self-limiting.

(A) Earthworm.

(B) A badger sett.

FIGURE 3.13: Examples of niche construction where life alters their environment to improve their survival prospects. Earthworms change the soil in their environment both physically and chemically which allows them to live on land without drying out (which would kill them), and badgers shelter in setts during the day and to keep warm during cold periods and remain safe from dangers.

In the early Daisyworld models niche construction plays a role in the maintenance of habitability. Early on in the model, with a cooler host sun, the black daisies experience an explosive growth due to the improvement of their own local environments. With their lower albedos, black daisies warm their local environments which in turn leads to a warmer global environment and thus pushes the temperature closer to the optimum temperature for daisy growth. White daisies are self-limiting under this cooler star as when they begin to grow, they cool their local environment thus stunting their own growth and spread. Once global temperatures become near optimal, the competition between daisy species results in temperature regulation. When the system is perturbed too far for the daisies to counteract, catastrophic loss of daisies occurs resulting in total extinction, and the temperature of the daisyworld increases to the now inhospitable abiotic value.

Niche construction also plays a role in the Guild model, where the microbes whose metabolic actions improve their local environment are more

likely to spread, thus increasing their positive impact on the shared global environment, as the benefits of their metabolism leak into the shared environment.

The key element for niche construction to be possible is that organisms must be able to form a porous barrier between themselves and the global environment.

3 .2 Rein control

Rein-control is a regulation mechanism first detailed in Saunders, Koeslag, and Wessels (1998) regarding the regulation of blood glucose levels, and later applied to Gaia in later versions of the Daisyworld model where the local environment was removed and all daisies shared only a global environment (McDonald-Gibson et al., 2008; Dyke, 2010). In this setup black and white daisies 'pull' the global environment in different directions with the result of regulating it. Black daisies grow better under cooler conditions and act to warm the environment whereas white daisies grow better under warmer conditions and cool the environment. This results in a feedback loop where black daisies will warm a cooler planet and white daisies will cool a warmer planet thus leading to regulation. The interplay between these two daisies species is imagined to be similar to two reins, each pulling the system in the opposite direction to the other and thus resulting in stability and regulation.

The Daisystat model (Dyke, 2010) demonstrates rein-control working on multiple parameters without pre-set 'ideal' values. As daisy species in Daisystat have growth rates peaking at different values for the parameters, the values these parameters are regulated at depends on the community of daisies alive at any time. Subgroups of daisies emerge which act to 'pull' the parameters in opposite directions.

3 .3 Sequential selection

Sequential selection is a proposed mechanism whereby a system perturbed towards its tolerable limit will reconfigure until an arrangement that brings the system back under control emerges. It is characterised by a series of trials over time that continue until stability is found. The Daisystat model (Dyke, 2010) exhibits sequential selection – when parameters are pushed too far for the current daisy community to survive, the system 'randomly reconfigures' – daisy species come into and out of existence as the temperature of their

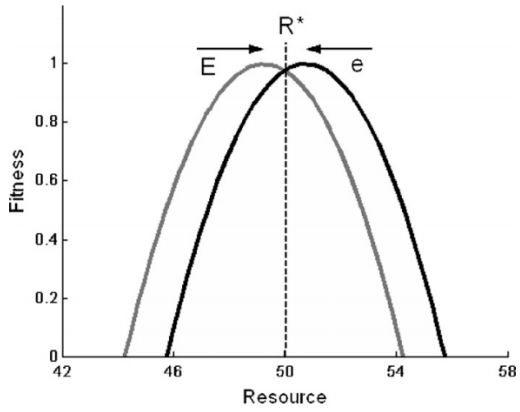


FIGURE 3.14: Diagram of rein-control (Dyke, 2010). The two lines show the growth curves for two different species, and the arrows represent the direction of each species' abiotic impact. The light grey species has a lower ideal resource value than the black species, and the grey acts to push the resource value higher, while the black acts to lower the resource value. With the actions of both these species, the resource level becomes stable at R*.

world changes, until a community emerges that acts to stabilise and regulate the temperature once again, at a different value to the one before. This behaviour is also shown in the Tangled Nature model (Christensen et al., 2002; Anderson and Jensen, 2005; Lawson, Jensen, and Kaneko, 2006; Laird and Jensen, 2006; Laird and Jensen, 2007) where after the collapse of a quasi-stable ecosystem, species appear and disappear during the 'quake' period, until a stable configuration is found where a 'core' group of species reinforce one another's growth rates and thus form a new quasi-stable ecosystem.

Figure 3.15 shows a visual metaphor for a sequential selection journey through the phase-space of a complex system, in this case applied to a planet (Lenton et al., 2018). The journey of the system is shown in black lines, moving through the phase-space. Most moves are small and remain within the local minima, where the smallest concentric rings are, however some move the system from one stable attractor, to another in larger regime shifts. The system spends most of its time in stable states, with time proportional to the stability of the state. Destabilising evolutionary innovations drive rapid transitions (the arrows) through unstable regions. The stability of a system is at a maximum where evolutionary dynamics and any geochemical processes happening on a planet push the planet towards the same stable attractor. External perturbations can also drive transitions to increasingly stable states. In Figure 3.15 the planet starts in an attractor that is not stable enough to

support complex life but then transitions to progressively more stable attractors, while, by luck, avoiding the very stable but uninhabitable 'Dead planet' attractor state. This 'dead' attractor could represent the aftermath of a 'runaway greenhouse' effect for example, perhaps the scenario that occurred on early Venus.

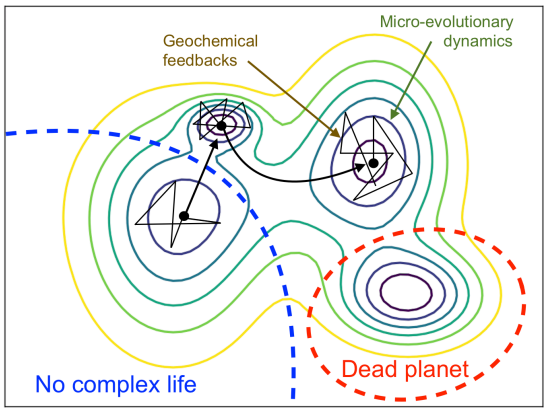


FIGURE 3.15: Diagram from Lenton et al. (2018) showing a representation of sequential selection. The contours represent changes in the stability of different system configurations, with the wells being the most stable points. The black lines represent the system's configuration which is changing via evolution and / or external perturbations, moving through the system configuration space. This movement is characterised by smaller moves within the local area of current stability and rarer large-scale events where the system rapidly moves from one potential well to another. On average in the system will 'find' points of increasing stability over time.

3 .4 Entropic arguments for Gaia

For a simple explanation of entropy, we can consider a bag of cables. Most houses have one lying about, filled with computer, camera, phone etc cables of various ages. If ever you need to retrieve one of these cables, they are almost always entwined with one another in an irritating way that takes some care and time to disentangle. This is entropy at work – there are more ways for the bag of cables to be tangled, than there are for them to be untangled, and so after time, we expect to find the bag of cables in a tangled state, as it is more probable. This fundamental law of the universe also has something to say regarding Gaia.

Entropic arguments for Gaia follow on from the Sequential Selection mechanism. Where sequential selection posits that ecosystem configurations will dissolve and reform following a perturbation, until a stable state is found, an Entropic argument for Gaia takes this a step further to stay that each subsequent quasi-stable ecosystem is statistically likely to be more complex and have a larger population than the one preceding it, and that over time, these stable states are expected to persist for longer and longer times, e.g the system will become less susceptible to perturbations.

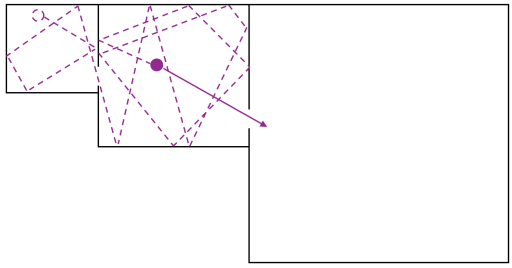


FIGURE 3.16: An analogy for explaining the tendency of some systems to increase in complexity over time. There are fewer system configurations that are simple, represented in the figure as the smallest box. A particle in that box with move about until is moves to a state of more complexity. There are more ways to be more complex, and so this box is larger. Therefore the particle is likely to spend longer in this box than the one before it. Should it move back to the smaller box it will quickly re-enter the larger box. The situation is the same for the next larger box. Thus as the complexity of the system is increasing over time so is the stability of the system.

The analogy of a particle in a series of boxes has been used to describe entropic hierarchies such as those demonstrated by the Tangled Nature Model (TNM), see Figure 3.16. We imagine that a particle is moving in a box, and in this box is a small hole to larger box, which itself has another small hole leading to another even larger box and so on. We imagine the particle moving about in these series of boxes, as we expect that after some time the particle will exit the smallest box moving into a larger one. In this larger box, with more space and more room for the particle it is likely to spend longer in this box than in the previous one. The same is true again for the next largest box and so on. The particle might move backwards to a smaller box, but after much time has passed we would expect to find the particle in the largest box available to it. In the case of the TNM, the boxes are ecosystem sizes, and the particle is the current configuration of the system. In short there are

more ways to have more diverse ecosystems than there are to have ecosystems consisting of only a small number of core members, therefore over time, we would expect to find systems of increasing complexity and stability due to the increasing entropic barriers mutants need to cross with increasingly complex ecosystems.

In the Gaian TNM version presented in Arthur and Nicholson (2017), not only are the inter-species dynamics important for determining a species growth rate but species also impact the habitability of their environment. Following a quake, when populations are low, biological effects on the environment will not greatly impact the species growth rate (a small number of organisms will not have a large impact on their environment). When populations increase however this species-environment influence will start to have a larger impact on species' growth rates. Therefore ecosystems that degrade their environment will become self-limiting and will have lower populations in average than those that improve their environment. As larger population ecosystems are less prone to quakes due to the larger entropic barrier they present to mutants, over time there is a larger probability of us finding an environment-improving ecosystem over an environment-degrading one. This entropic argument for Gaia is important as it helps explain why we might expect to find a planet hosting life to be Gaian rather than anti-Gaian, and why Gaian regulation need not be explained by natural selection (although of course the two must be compatible).

3 .5 Observer self-selection

Observer-self selection is the premise that our observations of our place in the universe are unavoidably biased by selection effects, as a specific environment was required for life to emerge on Earth and for humans to evolve from that life. This will be true for any intelligent life contemplating its origins. Without a certain history, a planet cannot support life, and so any life observing its surroundings will only be observing a narrow range of the possible outcomes of a planet's formation. It is obvious that life bearing planets are possible, as here we are, however the presence of Earth and ourselves does not easily inform us of the probability of such an occurrence (Watson, 2004).

This principle of observer selection bias is known as the 'Anthropic Principle' (Carter, 1974; Carter, 1983) and has been invoked to explain why the

FIGURE 3.17: A slightly whimsical example of observer self selection. To the cat his environment seems ideal, however the Earth required a certain history for the cat to exist – the formation of a solid crust for example, and a sun suitable for photosynthesis. The cat himself is also adapted to his environment, e.g. he has fur for warmth and teeth and claws for hunting prey.

universe formed in a such a way that allowed for complex life. If the fundamental constants of the universe were not within a very narrow range, our universe would be a very different place – elements heavier than Hydrogen and Helium might not be possible, or all stars would be massive with short lifespans removing the possibility for complex life to evolve over long periods of time. The 'weak Anthropic Principle' states that this apparent 'fine tuning' is the result of selection bias. Only in a universe where life is possible will there be lifeforms contemplating the matter and asking such questions. An alternative 'strong Anthropic Principle' claims that any universe will inevitably host life, however this hypothesis has far less support.

When contemplating Gaia, rather than fundamental constants of the universe, we are concerned with regulatory feedback loops, and specifically those involving life. Observer self-selection certainly does play a role in us being here on Earth, however how strong a role depends on how likely it was to have occurred at all. Is our Gaia a lucky Gaia or a probable one (Chapter 3)?

We only have the history of one planet with life – Earth, and the jury is still out on whether our neighbouring planets ever hosted life (see Chapter 6). No strong evidence has yet been found for extraterrestrial life and so our data is limited to one point – Earth. Without a statistical sample of inhabited planets we are limited in being able to test hypotheses – we cannot rewind the Earth and restart it to see if today's environment again emerges. However by examining Earth's long history, and combining these observations

with experiments run on simulated worlds, we can start to make some educated guesses on the likelihood of regulatory mechanisms emerging on a life-planet coupled system. Chapter 7 explores these questions in more detail and presents a model designed to shed some light on whether lucky, or probable Gaia might be closer to the truth.

4 Summary

In this Chapter I have given an overview of some of the key computer models designed to investigate the Gaia hypothesis, and of the mechanisms found in such models that play a part in regulation in a Gaian system.

The following Chapters add to the regulation and selection mechanisms that have been outline here. In Chapter 4 I will investigate a new variant of the flask model, which is the first model demonstrating 'single-rein control' as a regulatory mechanism arising from the interaction between life and the environment. In Chapter 5 I explore, using a simple model the hypothesis of selection by survival, first described in (Doolittle, 2014). The second part of this thesis will then consider planets beyond Earth and the search for extraterrestrial life in Chapter 6, and explore a new model of atmospheric regulation – the ExoGaia model – in Chapter 7.

Chapter 4

The Single-Flask model

So far in this thesis I have explored a number of regulation mechanisms that emerge in various Gaian computer models. In this Chapter I will introduce a new variant of the Flask model, imaginatively named the 'single-Flask model' because (you guessed it!) it has only a single flask environment. The inspiration for forming this model came from contemplating the parts of our Earth system that act, somewhat, as a well mixed global parameter, the atmosphere being the most obvious example. Although the climate differs in different parts of the world, the composition of our atmosphere, i.e. the concentration of CO_2, O_2 etc is overall on average the same wherever we are. The composition of the atmosphere is strongly influenced by life which participates in the regulation of various atmospheric gases. If all life shares the same global environment, and is unable to create any sort of niche construction or rely on group selection, how does regulation emerge under these circumstances? And what is the mechanism behind any such regulation? The model presented in this chapter comes some way in helping to answer these questions.

The work presented in this chapter was published in the Journal of Theoretical Biology, February 2017, titled "Multiple states of environmental regulation in well-mixed model biospheres" (Nicholson et al., 2017). I was the lead author on this paper. My contributions to the published work include writing the code used to generate the data contained within the paper, analysing the data, creating the graphs and writing the bulk of the text. The work is presented as its published form, only differing in the correction of a few typos found since publication and has been taken out of the journal formatting.

Multiple states of environmental regulation in well-mixed model biospheres

Arwen E. Nicholson, David M. Wilkinson, Hywel T.P. Williams and Timothy M. Lenton

Abstract

The Gaia hypothesis postulates that life influences Earth's feedback mechanisms to form a self regulating system. This provokes the question: how can global self-regulation evolve? Most models demonstrating environmental regulation involving life have relied on alignment between local selection and global regulation. In these models environment-improving individuals or communities spread to outcompete environment degrading individuals / communities, leading to global regulation, but this depends on local differences in environmental conditions. In contrast, well-mixed components of the Earth system, such as the atmosphere, lack local environmental differentiation. These previous models do not explain how global regulation can emerge in a system with no well defined local environment, or where the local environment is overwhelmed by global effects. We present a model of self-regulation by 'microbes' in an environment with no spatial structure. These microbes affect an abiotic 'temperature' as a byproduct of metabolism. We demonstrate that global self-regulation can arise in the absence of spatial structure in a diverse ecosystem without localised environmental effects. We find that systems can exhibit nutrient limitation and two temperature limitation regimes where the temperature is maintained at a near constant value. During temperature regulation, the total temperature change caused by the microbes is kept near constant by the total population expanding or contracting to absorb the impacts of new mutants on the average affect on the temperature per microbe. Dramatic shifts between low temperature regulation and high temperature regulation can occur when a mutant arises that causes the sign of the temperature effect to change. This result implies that self-regulating feedback loops can arise without the need for spatial structure, weakening criticisms of the Gaia hypothesis that state that with just one Earth, global regulation has

no mechanism for developing because natural selection requires selection between multiple entities.

1 Introduction

The Gaia hypothesis postulates that life on Earth interacts with abiotic processes to form a complex self regulating system that maintains habitable conditions on the planet (Lovelock and Margulis, 1974; Lenton, 1998; Lovelock, 2000). This is evolutionary ecology at the very largest spatial and temporal scales (Wilkinson, 2006). Critics of the theory argue that any organism acting to improve the habitability of the planet would have to contend with "cheaters" who do not contribute to regulation, or that a system would be just as likely to drive itself extinct as it would to drive itself towards stability (Doolittle, 1981; Dawkins, 1982). This leads to the question: how can self-regulation evolve in a way consistent with evolutionary theory? With only one Earth, and thus a lack of data to analyse, this question has been addressed using theoretical models. Hence we describe other models to put this study into context.

The Daisyworld model (Watson and Lovelock, 1983) was the first model to present global regulation emerging by local selection of individual level traits that contribute to global regulation. In the original Daisyworld there are two species of daisy – black daisies that have a low albedo and white daisies that have a high albedo. The growth of daisies is a function of temperature and all daisies have the same ideal temperature for maximum growth rate. Incoming radiation from a 'sun' that evolves in the manner of a typical main sequence star, heats Daisyworld. Daisyworld initially starts off too cool for any daisy growth, but as the sun evolves the incoming solar radiation becomes high enough for the surface temperature to allow daisy growth. Black daisies are the first to appear. By absorbing more solar radiation they warm their local environment encouraging their own growth and warming the global environment. When the temperature increases enough, cooling high albedo white daisies appear. The balance between the number of white cooling daisies and the number of warming black daisies maintains a constant habitable temperature in Daisyworld. As the solar luminosity increases the white daisies take over and keep the planet cool, until the incoming radiation is too high and all daisies die.

The Guild model (Downing and Zvirinsky, 1999), also demonstrates global regulation arising from local selection. In the Guild Model, individuals consume and excrete chemicals that appear in the system via an inflow. Which chemicals they consume and excrete are determined by an individual's genome. New 'species' (i.e. new genomes) arise via mutation during reproduction events. All individuals have maximum consumption levels when the ratio of chemicals is at a particular value. Individuals affect their local chemical ratios via their consumption and excretion and these effects diffuse to the global environment. As in Daisyworld, individuals that improve their local environment will be selected for, and this local selection contributes to global regulation. The Guild model finds that communities of individuals can exist together to create and regulate the preferred chemical ratios.

The Flask model (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010) removed a limiting assumption of Daisyworld and the Guild model that traits selected for at the individual level always improve the global environment. Instead the organisms in the system affect the abiotic environment as a byproduct of their metabolism, making these effects selectively neutral at the individual level. Instead of each individual having a distinct local environment, groups of individuals share a common local environment. During reproduction there is a small constant probability of mutation per locus P_{mut} so that over time new species arise via mutation. A spatial version of the model connected multiple local environments by inflows and outflows (Williams and Lenton, 2010; Williams and Lenton, 2008). Stabilising environmental regulation still emerged and this model argues for spatial structure creating conditions where limited higher-level selection can take place. In a connected environment, locations where local communities improve their environment achieve larger populations and thus can colonise and outcompete communities that degrade their environment leading to the spread of environment-improving communities and thus global regulation.

For local selection to take place on environment-related traits, local environments must be different. However, certain environments cannot be compartmentalised in a manner that seems conducive to local selection. The obvious example is the atmosphere (with its well mixed gases) but some aquatic environments are also potentially well mixed too. In this case it is not obvious where the local environments allowing for successful communities to develop would be, leading to motivation for a homogenous model of self-regulation.

Later versions of Daisyworld (McDonald-Gibson et al., 2008) and 'Daisystat' (Dyke, 2010) removed the local environment and found regulation of the abiotic parameters. In these models 'rein-control' (Clynes, 1969; Dyke and Weaver, 2013) is responsible for the environmental regulation. In one version of these models (McDonald-Gibson et al., 2008) two main subgroups dominate the system – one group that acts to increase the abiotic parameter while preferring this parameter to be low, and another group that acts to lower the abiotic parameter, while preferring this parameter to be high. With these two groups pulling the system in opposite directions, environmental regulation is possible for significant periods of time. The Daisystat model (Dyke, 2010) features the same 'rein-control' in this case regulating multiple abiotic parameters with a diverse array of species instead of the system being dominated by two main groups. In Flaskworld (Williams and Lenton, 2010), the effect of allowing different microbe species to prefer different abiotic parameter values was explored and it was found that the system showed periods of stability where the abiotic parameter stayed near constant. These stable periods were interrupted with rapid transitions where the abiotic parameter would often then stabilise at a different value to before. The system was stabilised by the 'rein-control' mechanism present in the Daisystat model.

The Daisystat model provides global regulation with a diverse population in the absence of spatial heterogeneity. However this model lacks mutation. Species begin reproducing when the environmental parameters allow them to, and all species are present at all times even if at vanishingly low levels. This means that as the environment changes, the system does not need to evolve new species to control or adapt to these changes, the species are already present and ready to start reproducing as soon as conditions allow. Therefore in Daisystat, the system cannot go extinct. This does not reflect real world biology where the existing population must evolve to cope with a changing environment and total extinction is a possibility. For this reason we follow the Flask model implementation of microbes with selectively neutral abiotic effects that reproduce and mutate allowing new species to appear in the system.

The atmosphere taken as a single entity has a flux of energy coming in as light from the sun, heat from the mantle and various chemicals spewed forth by volcanoes similar to the nutrient and abiotic parameter inflow in the Flask model. For something like the Earth's atmosphere a single well mixed environment would be a more accurate representation than local environments interacting with a global environment. CO_2 fluxes, for example,

at various points on the Earth do not vary wildly (ignoring the very small scale i.e. surrounding a currently active volcano) making a single flask Flask model a good approximation to the system.

The original Flask model (Williams and Lenton, 2007) was also a single flask environment, however the implementation of the model was quite different and the focus of the paper was on nutrient recycling and not abiotic regulation. In the original Flask model (Williams and Lenton, 2007) instead of microbes all having the same preferred value for a single abiotic parameter, there were two abiotic parameters and microbes had an encoded preference for a particular ratio of these two parameters. This ratio preference was not constant for all microbes and therefore not all microbes experienced the environment identically. When there is a universal preference for an abiotic parameter, this sets a constant target for regulation, where the preferences for abiotic parameter values differ, there is no such constant target. The target will change as the genetics within the population change. The microbes were able to evolve towards preferring the state of the current abiotic environment and exploit all the nutrients in the system. In this paper we instead focus on what happens in a system where the microbes cannot evolve towards preferring the current environment, and instead of a preferred ratio between two abiotic parameters that differs between different microbe species, we have a single abiotic parameter with a constant preferred value for this parameter, β that is the same for all microbes.

For our single flask Flask model we closely follow the implementation detailed in (Williams and Lenton, 2008) limiting the system to a single flask. We present a model of self-regulation of a purely global environment arising via evolution. This single Flask model allows for the possibility of rebel mutants disrupting the system, due to the lack of distinct environments and removes the issue of "cheater" species, due to the selectively neutral abiotic effects of the microbes. It is also possible for the system to drive itself to extinction – all scenarios being criticisms of the Gaia theory (Doolittle, 1981; Dawkins, 1982). The combination of assumptions presented here differs to what has been tried in previous models. The model has a shared preference for a single abiotic parameter, but lacks spatial structure as in the previous Flask models (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010). Mutation occurs in this model with a constant probability per

reproduction event, and the system can suffer from total irreversible extinction, differing from to the Daisystat (Dyke, 2010) and models by McDonald-Gibson (McDonald-Gibson et al., 2008). Finally, the model lacks local environments, differing from the original Daisyworld (Watson and Lovelock, 1983), and the Guild model (Downing and Zvirinsky, 1999).

In Section 2 of this paper we give a brief outline of the model (an in depth description can be found in Appendix A). Section 3 details the behaviour of the model for various important regimes. We present results both of typical individual simulations and for trends in systems with the same parameter settings. In Section 4 we discuss the results and provide parallels to behaviour found in the real world.

2 Model

In the Flask model (Williams and Lenton, 2010; Williams and Lenton, 2008), flasks contain an abiotic environment with parameters (that can be thought of as temperature, pH, salinity), and nutrients which are the substrates for metabolism, with a constant inflow and outflow of these abiotic parameters. The flasks are seeded with 'microbes' which consume the nutrients available and affect the abiotic parameters as a side effect of their metabolism. In turn the value of these abiotic parameters affects the microbes' ability to metabolise. In this paper we limit the system to a single flask.

'Microbes' are characterised by a binary genome. This genome determines what nutrients a microbe will consume and what it excretes (with the limitation that nothing may eat what it excretes). Microbes with the same genome are considered to be the same 'species'. As microbes consume nutrients and convert them to biomass, they are able to reproduce once their biomass reaches a reproduction threshold B_R. During reproduction there is a small constant probability of mutation per locus P_{mut} so that over time new species arise via mutation. Microbes die if their biomass drops to the starvation threshold B_D and there is also a probability of death by other causes P_D. The maintenance cost λ for each microbe is 1 biomass unit per timestep.

We refer to microbes with different genomes as being different 'species', however our model is essentially microbial, e.g. akin to the Earth during the Archean. In microbes, extensive horizontal gene transfer can make speciation a complex matter, and in the case of this model, it is the phenotype of the microbes that is important, rather than their genotype, which just determines which nutrients they eat and excrete. We have a rather small genome size in

this model and so minor changes usually associated with specific variation are not possible. Our model is best understood in terms of the 'genomes' of the flask 'microbes' as trait vectors, whereby the 'mutation' operator is just a simple way of introducing variation. The model mutations can represent quite large changes in metabolism that would in reality most likely involve a longer sequence of smaller mutations. In this context it is relevant that results from an ecology model called the Tangled Nature model, used for investigating stability in ecosystems, found that allowing for gradual changes in the phenotype of the agents in the model, rather than large scale changes each mutation, simply lead to the same dynamics slowed down (Andersen and Sibani, 2016).

As a byproduct of converting nutrients to biomass the microbes affect the abiotic parameters. Per unit of biomass created, the microbes change an abiotic parameter by a set amount (determined by their genome) in the range [-1, 1]. The environmental abiotic parameters in turn affect the rate at which microbes can consume nutrients. Each microbe, j, has a preferred level, β_j^i, for each abiotic parameter, i. β_{env}^i is the value of the i^{th} abiotic parameter. τ controls how sensitive the microbes are to the abiotic parameters. If $\tau = 0$, the microbes are not influenced by the abiotic parameters. For $\tau > 0$, the abiotic environment affects metabolism. The higher τ becomes the more sensitive the microbes become to their environment and thus for a high τ if the difference between each β_j^i and β_{env}^i is too large the microbes will be unable to consume nutrients. The quantity of nutrients a microbe is able to consume per timestep, C_j^{max}, depends on how closely each β_{env}^i matches β_j^i in the following way:

$$C_j^{max} = \psi_j C^{max} \tag{4.1}$$

$$\psi_j = e^{-(\tau p_j)^2} \tag{4.2}$$

$$p_j = \sqrt{\sum_{i=1}^{A} (\beta_{env}^i - \beta_j^i)^2} \tag{4.3}$$

where C^{max} is a constant determining the maximum rate of consumption for any microbe in ideal conditions, ψ_j is a microbe specific measure of the microbe's satisfaction with the current abiotic environment. A is the total number of abiotic parameters. As the β_{env}^i values move away from the ideal β_j^i values, C_j^{max} will become smaller meaning the microbes are able to ingest

fewer nutrients per timestep and for unfavourable enough conditions, they will be unable to consume anything.

The environment of the single flask is characterised by a constant inflow of nutrients and abiotic parameters, I_N and I_A, and a constant outflow O_N and O_A. In the absence of microbial activity the environment reaches a constant steady state with constant levels of nutrients and constant values for the abiotic parameters. After a preparation period t_{prep} to allow the system to come to equilibrium, the flask is seeded with 100 randomly generated individuals. For a single timestep the following actions are preformed:

1. Influx / outflux of nutrients and abiotic parameters
2. Microbe selected randomly for a death event
3. Microbe selected randomly for a nutrient consumption event
4. Microbe selected randomly for a biomass creation event
5. Microbe selected randomly for a reproduction event
6. Repeat steps 2 - 5 n times, where n is the total population of the system at the start of the current timestep.

In this way, on average, each microbe in the system will be selected for each event per timestep. We keep steps 1 - 5 separate in the code to introduce randomness into the model. We also neglect to consider any situations where particular genomes or consumption behaviours affect reproduction rates or death rates as can happen in real life.

We ran simulations of this single Flask model for various values for τ to demonstrate that a single well mixed flask can exhibit environmental abiotic regulation with two stable regimes for a certain range of τ. For each simulation we had $N = 4$ nutrients and $A = 1$ abiotic parameter, denoted as β (and referred to as 'temperature' throughout this paper) for our systems. We set $\beta_j = \beta = 150$ for each microbe, j, and the abiotic 'temperature' without microbe activity to $\beta_{env} = 100$. Throughout this paper we will refer to the nutrients in the system and the abiotic parameter separately. Although the nutrients present in a system part of the abiotic environment, we reserve this label for the abiotic 'temperature'.

For more details on the model presented in this paper see Appendix A .

TABLE 4.1: Survival % and average lifespan as a fraction of the total simulation length (10^5 timesteps) for a range of τ.

τ	Survival %	Average lifespan / 10^5	Standard deviation
0.00	100	1	0
0.005	100	1	0
0.01	100	1	0
0.015	100	1	0
0.02	50	0.75	0.32
0.025	18	0.33	0.38
0.03	9	0.20	0.33

3 Results

For a range of values for τ, a key parameter that controls the strength of the feedback between the environmental state and life, we ran 100 simulations, all identical apart from their initial random seed, and recorded how many of these 100 simulations survived (survival defined as having microbes alive at the end of the simulation) to 10^5 time steps. We then looked in closer detail at these surviving simulations.

Table 7.1 shows the survival rate of simulations for different values of τ. We see that the survival rate of the system quickly starts to drop off above $\tau = 0.015$.

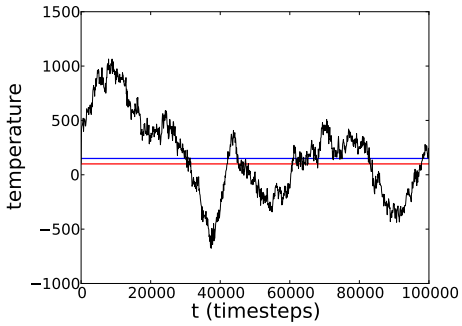
Table 7.1 also shows the mean lifespan for various τ along with the standard deviation. For low τ all the simulations survived to the end, but as τ increases the survival rate decreases and so does the average lifespan.

We find that there are three ways in which the microbe population of the system can be limited – nutrient limited, high temperature limited and low temperature limited. Which of these regimes dominates the system depends on the value of τ.

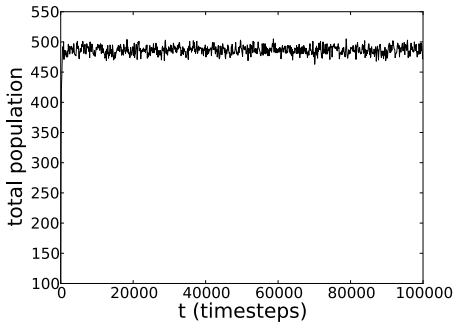
3 .1 Nutrient limitation for $\tau = 0$

In a nutrient limited regime the microbes consume all the available nutrients. Once the nutrients are depleted the population can no longer grow and the microbe population will stabilise such that the flow of incoming nutrients is enough to support the population, i.e. the system reaches the carrying capacity determined by the nutrient input. This characterises a key aspect

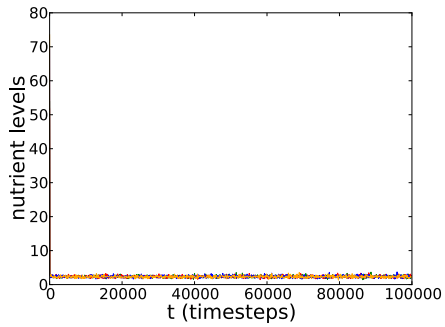
of many real-world systems where the tendency for biological populations to proliferate if conditions are good leads to a reduction of resources which then becomes a stable state – a process called 'biotic plunder' by (Tyrrell, 2004), and achieves a zero-net growth isocline (ZNGI) (Tilman, 1980). In a $\tau = 0$ system, i.e. the microbes are indifferent to the abiotic temperature, nutrient limitation is the only way the system becomes limited.



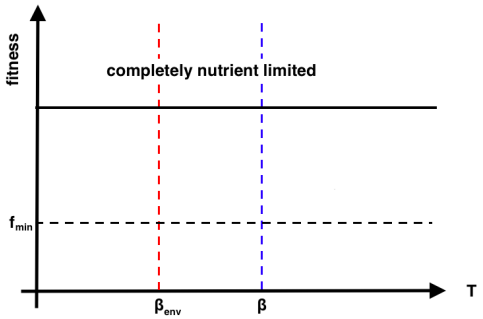
(A) $\tau = 0.00$ temperature plots.



(B) $\tau = 0.00$ population plots.



(C) $\tau = 0.00$ nutrient stocks plot.



(D) $\tau = 0$ fitness diagram.

FIGURE 4.1: Example simulation of a single $\tau = 0$ system. In a) and d) the blue line represents β and the red line represents β_{env}. The temperature a) has no general trend, the total population b) quickly rises and stabilises at the carrying capacity. The nutrient stocks c) quickly deplete and remain at near zero levels. The fitness doesn't depend on temperature so the fitness d) is a constant.

Figure 4.1 shows a single simulation for $\tau = 0$. In Figure 4.1b the temperature has no overall trend but is a random walk as the microbes are not affected by its value. The changes in temperature come from the byproducts of the microbes' metabolism. For every unit of biomass produced each microbe will add a set value to the temperature parameter as determined by their genome. Genetic mutation is occurring within the population and so new species with different affects on the temperature regularly appear. For

$\tau = 0$ the fitness, which we define as the rate of biomass production per microbe, per timestep, is at the maximum value for any value of T, meaning that the temperature is selectively neutral and so the system's temperature is effectively an unbiased random walk, determined by the current populations genomes, and changing with genetic variation. When the system is nutrient limited, the system is still producing mutants at the same rate per microbe. This means that the total abiotic effect of the microbe ecosystem will be constantly changing as new mutants with differing abiotic impacts appear preventing the temperature from stabilising.

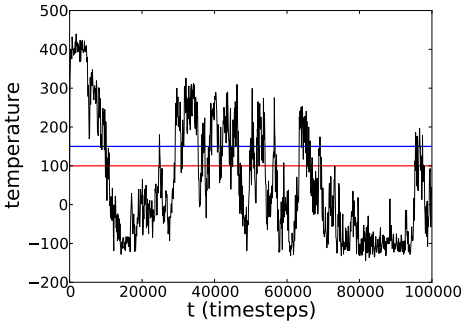
From Figures 4.1b and 4.1d we see that the population quickly reaches a maximum value and stays there and that the nutrient stocks are quickly reduced to near zero and also stay at that level. The total population possible in a system is determined by the nutrient flow.

Figure 4.1d shows a cartoon plot of temperature against fitness with respect to the abiotic temperature, all else being equal. f_{min} represents the minimum fitness, here defined as the number of offspring produced per individual per timestep, required for the microbes to maintain a constant population, i.e. the rate of reproduction matches the rate of death. As the value of the temperature does not affect fitness for $\tau = 0$, the fitness of the microbes is a constant independent on T. Note that the temperature in this model is arbitrary and does not correspond to real world temperatures, and so it is the behaviour of the temperature that is important, not the value.

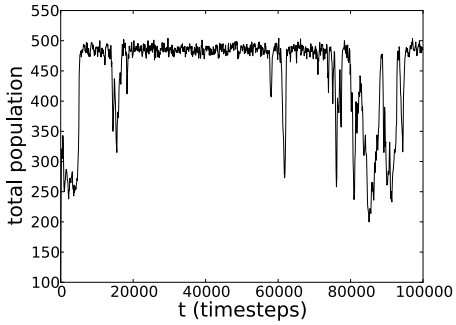
3 .2 Nutrient and temperature limitation for $\tau > 0$

For $\tau > 0$ the microbes fitness is no longer constant for all temperature, see Equation (4.3). In $\tau > 0$ systems, the system can still become nutrient limited if the average effect per microbe on the abiotic temperature, ϵ_{avg}, is small enough to allow the microbes to exhaust the nutrient stocks. We calculate ϵ_{avg} by summing up all the abiotic effects for all the microbes, and then dividing by the total population of the system to get the average metabolic effect per microbe. As τ increases and the microbes become more and more sensitive to their environment nutrient limitation becomes less likely, and when it does happen it quickly transitions to a temperature limited regime instead.

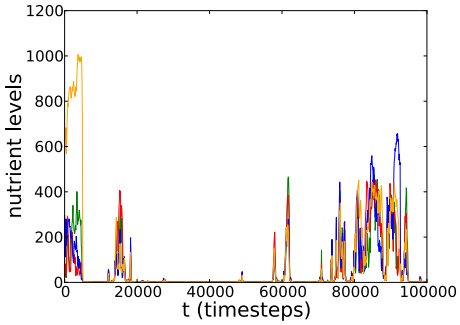
Figure 4.2 shows a $\tau = 0.005$ simulation that demonstrates nutrient limitation and temperature limitation. There are periods in Figures 4.2b and 4.2c when the system is not nutrient limited as the total population falls below the maximum and the nutrient stocks are not completely exploited



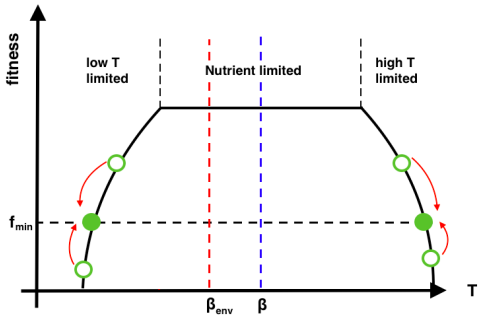
(A) $\tau = 0.005$ temperature plot.



(B) $\tau = 0.005$ population plot.



(C) $\tau = 0.005$ nutrient stocks plot.



(D) $\tau = 0.005$ fitness diagram.

FIGURE 4.2: Temperature, population and nutrient stock plots for an individual $\tau = 0.005$ system. In a) and d) the blue line represents β and the red line represents β_{env}. We see regions of temperature limitation a) where the population b) drops to lower than the carrying capacity, and the nutrient stock c) are higher. The fitness d) now depends on the temperature for extreme temperatures.

i.e. at $t = 0 - 500$ where the system is high temperature limited, and $t = 70,000 - 95,000$ where the system is low temperature limited. At low τ the system is mainly nutrient limited, but as the temperature goes towards the extremes at which the microbe's can survive, the system becomes temperature limited, and the fitness curve falls away from the maximum, shown in Figure 4.2d. When temperature limited, the system is in a negative feed back loop, with the stable point at the temperature that allows the minimum fitness required for a stable population. The green circles in Figure 4.2 represent the system at various temperatures. There are two points on the fitness curve where the temperature is in a semi-stable state – a state that persists for significant time spans but is prone to sudden transitions to another state. These semi-stable states occur where the fitness curve intersects the f_{min} line. Where these two lines cross we find the the upper and lower temperature limits. At these points green circles are filled to represent that the system

temperature is semi-stable for this T. At other points on the fitness curve the system temperature is not stable, represented by non-filled circles.

The two temperature regimes, high and low, work as follows:

- **High Temperature Limited Regime**

  The high temperature regime supports a population of microbes whose collective effect on the environment is to heat it. As the microbes consume nutrients and create biomass the temperature increases until the microbes become unable to consume nutrients due to the temperature being too extreme. At this point with no microbes creating biomass, and the constant flow creating a cooler environment, the temperature begins to fall until it reaches the point where microbes are able to consume nutrients again and the cycle repeats. In this way the system can be thought of as bouncing off an upper temperature limit set by how extreme a temperature the microbes can still metabolise in. In the high temperature limited regime ϵ_{avg}, is positive – i.e. on average a microbe has a heating effect.

  In a system limited by high temperature the total population and ϵ_{avg} are highly negatively correlated. If a population has a certain ϵ_{avg} and a new microbe mutates into existence that causes ϵ_{avg} to increase, then depending on the size of the temperature increase the microbes' metabolism may slow to levels too low to maintain a constant population, in which case random deaths will reduce the population, or, if the temperature increase is extreme enough, metabolism can halt entirely. This will lead to individuals starving and the population will drop. With a lower rate of metabolism or no metabolism happening at all the temperature of the system will start to drop due to the inflow and outflow of temperature to the system. At a certain point the temperature will drop enough that the microbes will be able to start consuming nutrients again and the system will continue at roughly the limiting high temperature but supporting a lower population.

  Time scales are important in these events as if the temperature change is extreme enough that metabolism halts entirely, the whole population will very quickly die and so the system can only tolerate short lived excursions from habitable temperatures. For a less extreme temperature change that still allows metabolism to take place (albeit at a rate below the maintenance level) then the system can survive longer as it will take longer for the microbes to starve to death or, failing starvation,

the random death events will reduce the population. In general, any affects that act to push the temperature beyond habitable limits must be counteracted quickly to avoid total extinction.

Conversely if the effect of the new mutant was to lower ϵ_{avg}, the temperature would drop and thus the microbes would consume more nutrients, the population would increase, raising the temperature with it until it stabilised at around the limiting high temperature, this time supporting a higher population than before.

- **Low Temperature Limited Regime**

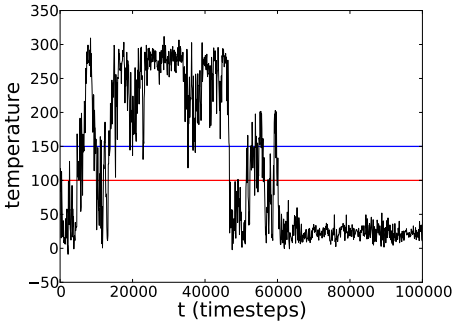
  The low temperature regime is almost the mirror image of the high temperature regime. In the low temperature limited regime ϵ_{avg} is negative – i.e. on average a microbe has a cooling effect. In this case the total population of microbes and ϵ_{avg} are positively correlated. If a microbe mutates into existence that causes ϵ_{avg} to increase, the population will increase, and if the mutant acts to decrease ϵ_{avg} the population will decrease.

As τ increases, temperature limitation becomes more important. For a higher τ, the microbes are more sensitive to their abiotic temperature and nutrient limitation is possible for a smaller range of T. When nutrient limited, the system has a higher total population than when temperature limited, so mutants appear at a faster rate. This combined with the smaller nutrient limited T range means that the system can quickly random walk out of nutrient limitation and become temperature limited. So as τ increases, nutrient limitation dominates systems less, and temperature limitation takes over. Figure 4.3 shows two systems, a $\tau = 0.01$ system and a $\tau = 0.015$ system, and shows a higher amount of temperature limitation for the higher τ.

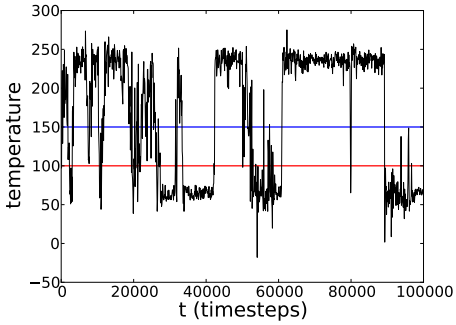
Comparing Figures 4.3c and 4.3d we see that for $\tau = 0.015$, the periods of nutrient limitation (seen where the nutrient stocks are close to zero) are less frequent and of shorter duration than they are for $\tau = 0.01$.

3 .3 Temperature limitation dominates for $\tau \geq 0.02$

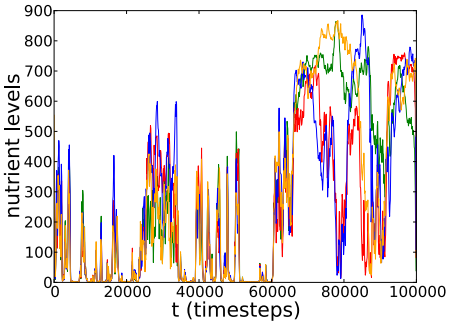
As τ increases, the span of temperature where the microbes are nutrient limited shrinks further, so that the system becomes dominated by temperature limitation. The asymmetry in the model set up also begins to have a noticeable affect on the temperature limited regimes. As β_{env} is cooler than the



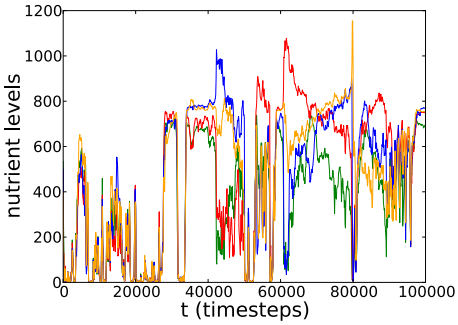
(A) $\tau = 0.01$ temperature plot



(B) $\tau = 0.015$ temperature plot



(C) $\tau = 0.01$ nutrient stocks plot



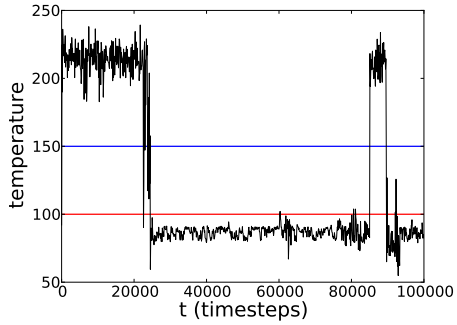
(D) $\tau = 0.015$ nutrient stocks plot

FIGURE 4.3: Plots for two individual systems, one at $\tau = 0.01$ and the other at $\tau = 0.015$. In a) and b) the blue line represents β and the red line represents β_{env}. As τ increases, temperature limitation becomes more likely than nutrient limitation.

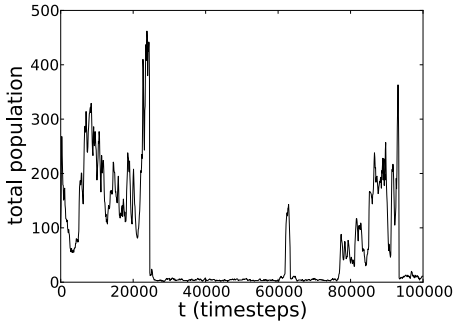
microbes' preferred temperature β the total cooling effect needed by the microbes to become low-temperature limited is less than the total heating effect required to become high-temperature limited. For low τ where the temperature range in which the microbes can function in is large, this does not have much effect, but as τ decreases and the high and low temperature limits contract towards β, this starts to have an effect.

As the cooling needed to become low-temperature limited is less, the total population that this low temperature limited regime can support becomes lower and lower as the limiting low temperature increases. If a mutant then arises that causes ϵ_{avg} to cool more strongly, the population has to shrink to counteract this, and with an already small population this is more likely to drive the system to extinction than for the high temperature limiting regime, which can support a higher population. This means that as τ increases the low temperature limiting regime becomes less stable and the non-extinct systems are far more likely to be found in the high-temperature limiting state. This behaviour is due purely to the fact that β_{env} is lower than β. Were β_{env}

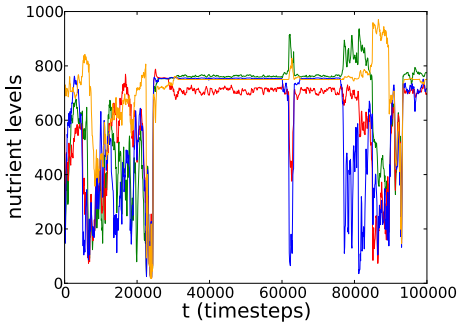
higher than β, we would see the same behaviour but flipped – the high temperature regime becoming less stable than the low temperature regime with increasing τ.



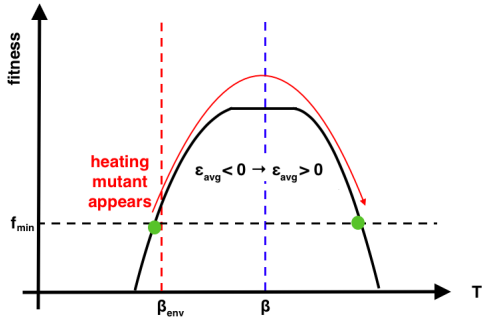
(A) $\tau = 0.02$ temperature plot.



(B) $\tau = 0.02$ population plot.



(C) $\tau = 0.02$ nutrient stocks plot.

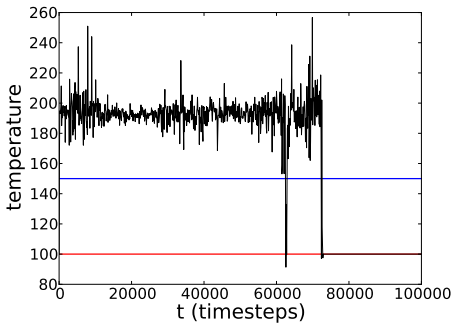


(D) $\tau = 0.02$ fitness diagram.

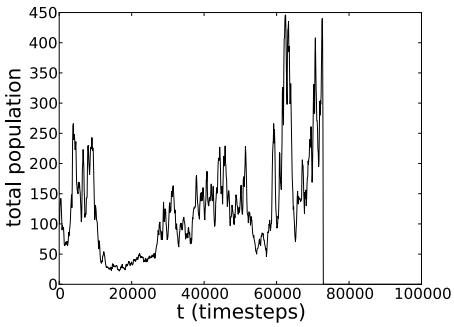
FIGURE 4.4: An individual $\tau = 0.02$ system. In a) and d) the blue line represents β and the red line represents β_{env}. Note in a) and b) when the system is limited by low temperature, the total population is very low. d) shows the nutrient limiting range shrinking. The red arrow indicates the system moving straight from low temperature limitation to high temperature limitation.

Figure 4.4 shows a $\tau = 0.02$ system that demonstrates this asymmetry. We see in the population graph, Figure 4.4b that the total population is much lower when the system is low temperature limited, than it is when the system is high temperature limited. We also see some very clear transitions between low temperature limitation and high temperature limitation without even a short a period of nutrient limitation in between. The higher τ value means there is a much smaller range of temperature where the system can be nutrient limited, so a mutant microbe acting to change $\epsilon_{avg} < 0$ to $\epsilon_{avg} > 0$ doesn't have to have as strong an effect for the system to move through nutrient limitation temperature range and become temperature limited on the other side, as Figure 4.4d demonstrates. From Figure 4.4c we see that there are always

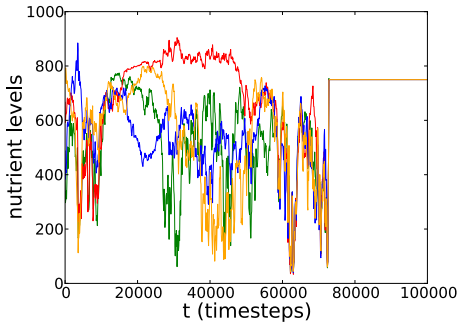
nutrients available. None of the stocks are ever fully depleted, the microbe ecosystem is never able to fully exploit the nutrient resources. If β and β_{env} were close enough, the microbes would be able to consume all available nutrients and become nutrient limited, but for $\tau = 0.025$ the temperature range that allows for nutrient limitation is very narrow so the system quickly gets knocked out due to mutants perturbing the system and pushing it to a temperature limited regime.



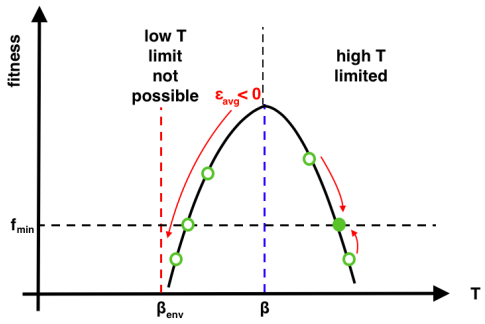
(A) $\tau = 0.03$ temperature plot.



(B) $\tau = 0.03$ population plot.



(C) $\tau = 0.03$ nutrient stocks plot.



(D) $\tau = 0.03$ fitness diagram.

FIGURE 4.5: Plots for an individual $\tau = 0.03$ system that goes extinct. In a) and d) the blue line represents β and the red line represents β_{env}. d) shows that the low temperature regime is now not possible.

Increasing to $\tau = 0.03$ and the asymmetry of the system now means that the high temperature becomes the only stable limitation regime. The temperature span for the nutrient limitation regime has reduced so much that the system will very quickly random walk away from this regime, and the lower temperature limiting regime T value is now above β_{env} (where the fitness curve intersects the f_{min} line in Figure 4.5d). This means there is no negative feed back mechanism for maintaining the system for a temperature below β. If the temperature falls below β and the microbes act to cool, then the temperature will decrease until the microbes begin to die off. As $\beta_{env} < \beta$ however,

now there is nothing to pull the system back towards β, the system will be pulled towards β_{env}, which is now too cool for any microbes to survive and the system will go extinct. The only way for the system to avoid extinction for $T < \beta$ is if $\epsilon_{avg} > 0$. In this case as the microbes heat the system, the temperature will increase towards β, increasing the fitness, increasing the total population and therefore accelerating the heating in a positive feedback loop, until $T > \beta$, and the system becomes high temperature limited in a negative feedback loop.

We can see in Figure 4.5a one time at $t = 65,000$ where the system is able to recover from $T < \beta$. In this case a mutant acting to change $\epsilon_{avg} < 0$ to $\epsilon_{avg} > 0$ appears and prevents the system from going extinct, but the system is not so lucky a second time, and goes extinct the next time $T < \beta$. The likelihood of producing a mutant depends on the reproduction rate and the population size and hence when the microbes' metabolism is constrained by temperature the reproduction rate is low. The high nutrient stocks present in the system however create a potential for rapid growth if a 'good' mutant appears, i.e. one that moves the temperature closer to β. Referring back to Table 7.1 we see that for $\tau = 0.03$ the survival rate for 10^5 timesteps was 9%, so systems that are able to recover are the minority. Again, Figure 4.5c shows that the nutrient stocks are never depleted, the microbes are unable to stay within the very narrow nutrient limited temperature range.

3 .4 Waiting time for 'Quakes'

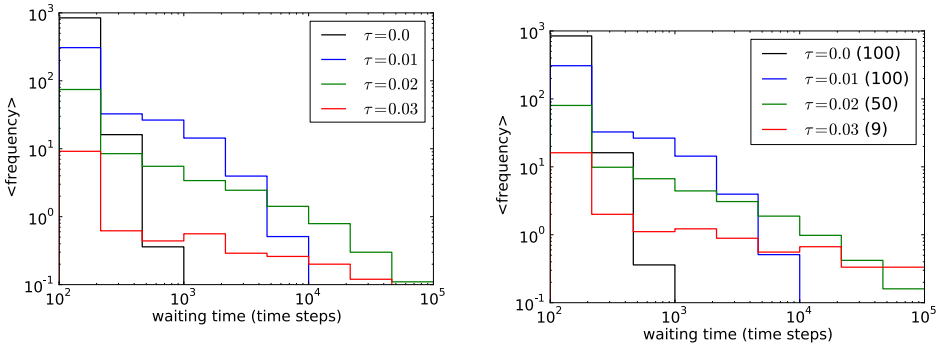
We can look at waiting time statistics for 'quakes' – a period where the system's temperature is not stable – to get an idea of how long the quasi-stable periods last within systems with various τ. For the purposes of the following analysis we define a quake in the following way:

$$quake = \begin{cases} 1, & \text{if } \left| T_{avg}^{prev} - T_{avg}^{cur} \right| > 5 \\ 0, & \text{otherwise} \end{cases} \tag{4.4}$$

where a value of 1 means a quake took place, and a value of 0 means the temperature is remaining stable – no quake. T_{avg}^{prev} is the temperature averaged over the previous 100 timesteps, and T_{avg}^{cur} is the temperature averaged over the next 100 timesteps. We compare T_{avg}^{prev} to $T_{avg}^{cur} \pm 5$ as some small temperature fluctuation does occur during stable periods so to compare the two with no buffer would lead to an artificially high number of quakes being recorded.

Using this method we can record the times at which quakes occurred in a system. $\pm$ 5 is chosen as it is large enough to take into account fluctuations that happen within a stable period, but small enough that quakes are noticed. Changing $\pm$ 5 to some other limit does not qualitatively change the results much, but quantitively the recorded number of quakes for all systems will increase if the limit is reduced, and will decrease a little if increased until the limit gets so large that quakes become unidentifiable.

The value of each waiting time bin in the histograms is divided by the number of simulations included.



(A) Frequency of quakes for all simulations.

(B) Frequency of quakes for only non extinct simulations.

FIGURE 4.6: Histograms showing the average frequency of waiting times for quakes for different τ. The number of non-extinct simulations in b) for each τ is given in brackets in the legend. Note that both the x and y axis are logarithmic.

Figure 4.6 shows histograms of the average frequency of waiting times for quakes for 4 values of τ = 0.00, 0.01, 0.02, 0.03. Figure 4.6a shows a histogram for all simulations while Figure 4.6b shows a histogram including only data from non extinct simulations. This allows us to look for characteristics in the 'successful' systems for various τ. We want to understand what behaviours a system needs to have in order to avoid extinction. We are looking at the the Gaia hypothesis from the point of view of a planet that has successfully had uninterrupted life for billions of years. We could be incredibly lucky, and our planet might, if 'reset' and run a 100 times, usually be doomed to total extinction, or perhaps every 100 times life would emerge and successfully regulate the planet to maintain habitable conditions. As we don't know which scenario we are in, it is useful to look for signatures in 'successful' systems for both scenarios (those likely to survive and those unlikely to survive) to see how we might be able to tell them apart. For each non extinct simulation for a

particular τ the waiting times for quakes are measured and binned, and then these bins are divided by the number of non-extinct simulations to give an estimate of how many times per simulation for a particular τ we can expect to wait a certain period of time for a quake. Note in Figure 4.6 that both the x and the y axis are plotted to log scale. Also note that because each simulation ends at $t = 10^5$ if a simulation lasts in a stable period for the whole simulation, the number of quakes would be 0 and thus in the plots in Figure 4.6 a lower frequency of waiting times means a more stable system as it indicates the stable periods of the system have remained mostly uninterrupted.

Figure 4.6 shows a histogram of waiting times for $\tau = 0, 0.01, 0.02, 0.03$. We see that the frequency of short waiting times for $\tau = 0$ is high. This frequency drops until just after 10^3 timesteps the frequency is 0. This agrees with previous plots showing no abiotic temperature regulation for $\tau = 0$. When $\tau = 0$ the microbes are not regulating the environmental temperature, so the temperature is free to wander. 'Quakes' in this scenario regarding the temperature no longer make sense as the temperature is never really stable but measuring for 'quakes' we would expect them to be frequent and for there to be short waiting times between them, which is what Figure 4.6 confirms.

For $\tau = 0.01$ the microbes are regulating the environmental temperature and the system can exhibit both temperature limitation and nutrient limitation. Here we see that longer waiting times occur and the shorter waiting times are less frequent than for the $\tau = 0$ case. This demonstrates that on average, for simulations with $\tau = 0.01$ we can expect longer periods of temperature stability with fewer quakes, however frequency of quakes drops to 0 for waiting times longer than roughly 10^4 timesteps.

For $\tau = 0.02$ we see that short waiting times for quakes happen at an even smaller frequency than for $\tau = 0.01$. Across almost all waiting times, the frequency of quakes is lower for $\tau = 0.02$ than for $\tau = 0.01$. This tells the story of a system with longer periods of stability and fewer quakes. From Table 7.1 recall that the survival rate for $\tau = 0.02$ is low at 28%. It is not therefore that at $\tau = 0.02$ the microbes are far better at keeping the environmental temperature from fluctuating than they are at $\tau = 0.01$, but that for a $\tau = 0.01$ system the more lenient restrictions on the microbes means that the system is better able to recover from a quake, but in a $\tau = 0.02$ case, quakes come with a larger probability of total extinction. So for $\tau = 0.02$ simulations with a lower level of quakes will have a greater probability of surviving. The relationship between frequency and waiting time for $\tau = 0.02$ in Figure 4.6

shows a roughly linear relationship suggesting that there is a power law relationship. If the frequency of quakes goes as $f_q \propto t^{-\alpha}$ where t represents time, and α is some constant, we can take the log of both sides to find a linear relationship in log-log space which is indicative of a power law.

For $\tau = 0.03$ we see that the frequency of all waiting times for quakes is very low, and with only 9% of the simulations avoiding extinction, this shows a more extreme version of the $\tau = 0.02$ case.

Comparing Figures 4.6a and 4.6b we can see that including only non-extinct simulation has the effect of 'flattening' the frequency curve, making it less steep and increasing the frequency of quakes for longer waiting times. When we include the data from simulations that went extinct, it lowers the quake frequency as an extinct system cannot quake, and it makes the high τ systems appear less prone to quakes than they are in reality.

3 .5 Population, Temperature and ϵ_{avg}

To get a clearer understanding of which regimes (nutrient limiting, high temperature limiting or low temperature limiting) are dominating the systems we plot the average microbe effect on the temperature, ϵ_{avg}, vs the temperature and vs the total population of the system for various τ. ϵ_{avg}, and the total population of the system are correlated when the system is in a temperature limiting regime – negatively correlated in the high temperature limiting regime and positively correlated in the low temperature limiting regime. Thus we expect to see (in a high temperature limiting scenario) that as ϵ_{avg} increases, the total population decreases.

Figure 4.7 shows ϵ_{avg} vs total population for the data from all non extinct simulations over a range of τ. We see for $\tau = 0$, the total population remains constant for any value of ϵ_{avg} which agrees with previous results. We can clearly see the nutrient limited regime for very low τ start initially wide and become increasingly narrower as τ increases. For $\tau = 0.005$ we clearly see both the low and high temperature regimes, the left curve showing the total population increases for an increase in (negative) ϵ_{avg} and the right curve showing the total population decreasing for increasing (positive) ϵ_{avg}. These two curves are slightly asymmetrical and this is due to β_{env} being cooler than β. This means that to become higher temperature limited a higher population for any ϵ_{avg} is needed than for the corresponding negative ϵ_{avg}.

As τ increases and the microbes become more sensitive to their environment the left hand side of the curves in Figure 4.7 become less populated.

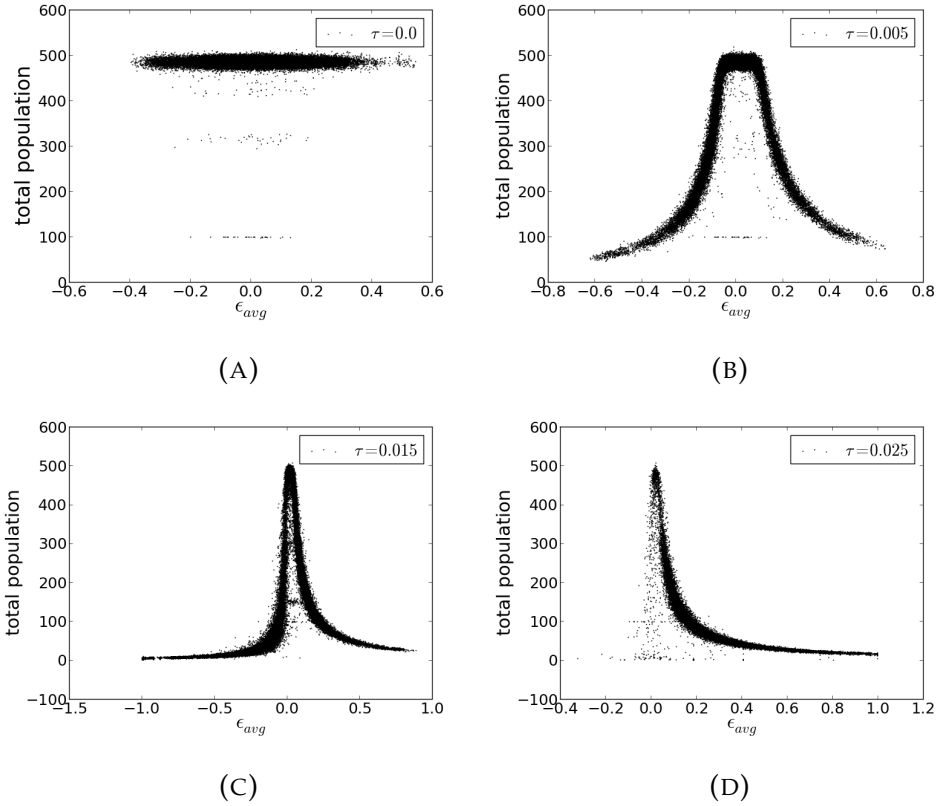


FIGURE 4.7: Plots showing ϵ_{avg} against total population for various τ. Total population is constant for varying ϵ_{avg} when the system is nutrient limited, however for temperature limited, the population must adjust as ϵ_{avg} changes to keep the total effect constant.

The net cooling needed to become low temperature regulated is smaller than the net heating to become high temperature limited and as τ increases the microbes need to keep a tighter control on their abiotic temperature and the upper and lower temperature bounds contract towards their ideal temperature β. Therefore, in order to survive, as τ increases, heating their abiotic temperature becomes a better strategy for the microbes as the high temperature limiting regime can support a higher number of microbes increasing their ability to adapt to new mutants making this regime more stable than the low temperature limiting regime. Thus we see that surviving simulations tend to have adopted a high temperature limited regime.

Figure 4.8 shows similar plots this time for ϵ_{avg} vs temperature. Here we see for $\tau = 0$, there is a linear relationship as expected – the total population remains constant and so changing ϵ_{avg} has a linear effect on the temperature. As τ increases we see a step like function, where for low and high ϵ_{avg} the

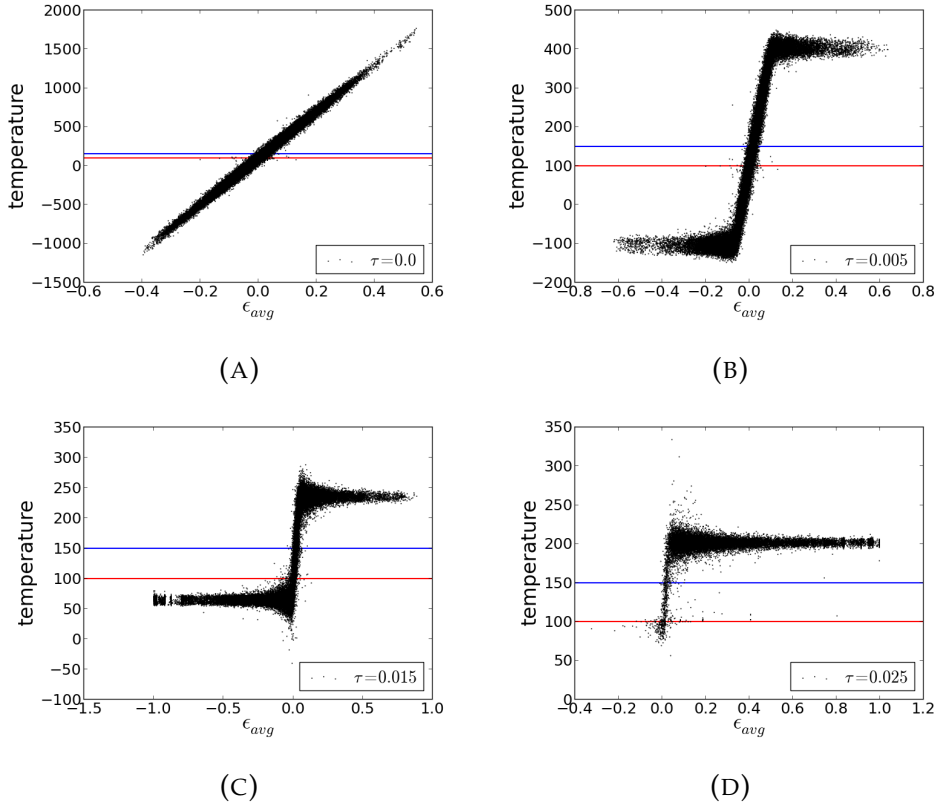


FIGURE 4.8: Plots showing ϵ_{avg} against the system temperature for flasks hosting life for various τ. The blue line represents β and the red line represents β_{env}. When the system is nutrient limited the temperature changes linearly with ϵ_{avg}, however during temperature limitation, the temperature remains constant for changing ϵ_{avg}.

temperature remains constant, and for a region of ϵ_{avg} around 0, there is a linear relationship – this is the region where the system is nutrient limited. As τ increases, this transition between the low and the high temperature limits becomes steeper showing that as τ increases, the system becomes increasingly less likely to find itself nutrient limited. We also see that increasing τ leads to the high and low temperature limits to contract towards β as the microbes habitable temperature range shrinks. Again we can see that for high τ, the system is more likely to be in the high temperature limited regime.

3 .6 Changing the environmental abiotic temperature

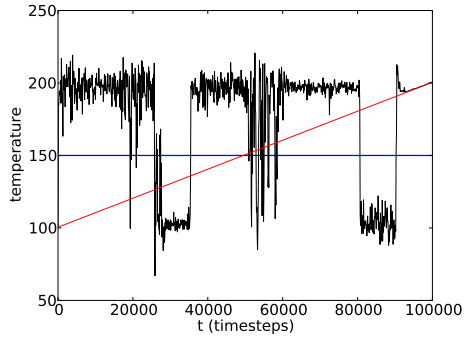
We investigated the effect of gradually increasing or decreasing the temperature for a range of τ. We found that temperature regulation is maintained in the face of a changing temperature, and microbes are able to keep the temperature habitable after the environmental equilibrium temperature would

TABLE 4.2: Heating and cooling survival % and average lifespans as a fraction of the total simulation length (10^5 timesteps) for a range of τ. Comparing with Table 7.1 we see that heating increases the survival % and cooling decreases it.

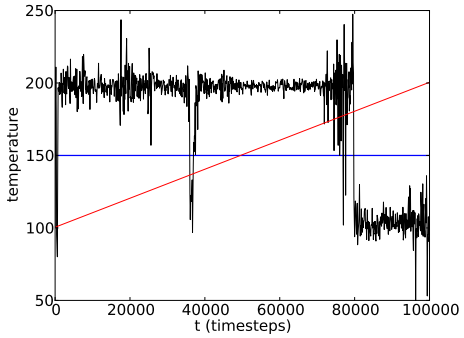
	Heating			Cooling		
τ	Survival %	Average lifespan / 10^5	Standard deviation	Survival %	Average lifespan / 10^5	Standard deviation
0.00	100	1	0	100	1	0
0.005	100	1	0	100	1	0
0.01	100	1	0	96	1	0.01
0.015	100	1	0	13	0.60	0.26
0.02	87	0.95	0.21	9	0.32	0.30
0.025	19	0.46	0.47	9	0.20	0.32
0.03	2	0.15	0.31	4	0.01	0.22

have become uninhabitable. However when quakes occurred, the system was highly susceptible to extinction once the equilibrium temperature was no longer habitable. Table 4.2 shows the survival and lifespan statistics for cooling the system from $\beta_{env} = 100$ to $\beta_{env} = 50$, and heating the system from $\beta_{env} = 100$ to $\beta_{env} = 200$.

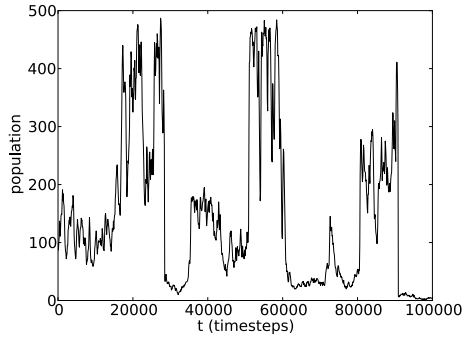
When changing β_{env} from 100 to 200, the environmental temperature is closer to $\beta = 150$, the preferred temperature of the microbes, during the experiment than when $\beta_{env} = 100$ for the entire experiment. This allows the system to become nutrient limited more often. Typically the temperature limited regime with the largest distance to β_{env} will support a higher population, as more microbes are required to achieve the required heating / cooling for temperature limitation. Recall Figure 4.4 where the population supported during the low temperature limited regime was significantly lower than the population supported during the high temperature limited regime. While $\beta_{env} < \beta$ the high temperature limiting regime can on average support a higher population, however when the environment has warmed so that $\beta_{env} > \beta$, the low temperature regime becomes able to support a higher population. As τ increases, the system becomes highly susceptible to quakes. Recall from Figure 4.5 that for $\tau = 0.03$ the low temperature limiting regime was no longer possible. When we change from $\beta_{env} = \beta - 50$ to $\beta_{env} = \beta + 50$ we change which of the temperature limiting regimes is possible. In order for a $\tau = 0.03$ system to survive heating, it must transition at a correct time from high temperature limitation to low temperature limitation. $\tau = 0.025$ and



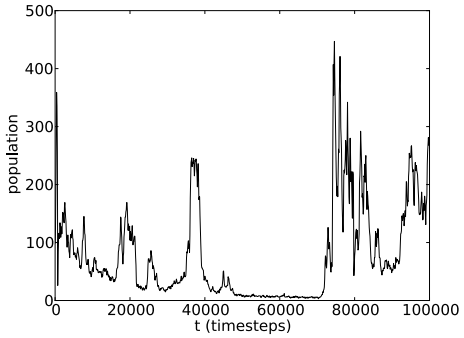
(A) $\tau = 0.025$ temperature plot.



(B) $\tau = 0.025$ temperature plot.



(C) $\tau = 0.025$ population plot.



(D) $\tau = 0.025$ population plot.

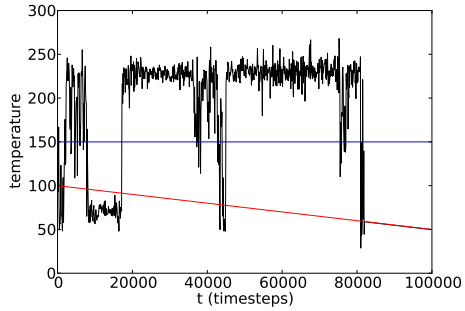
FIGURE 4.9: Heating the system with $tau = 0.025$.

$\tau = 0.03$ systems are already highly susceptible to extinction during quake events so adding a necessary quake in order to survive further reduces the probability of survival.

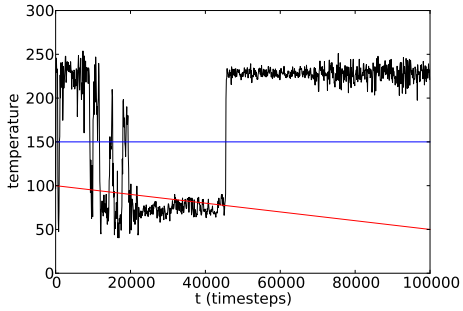
Figure 4.9 shows two $\tau = 0.025$ systems undergoing heating. In Figure 4.9a we can see that the system transitions to the high temperature limitation regime towards the end of the experiment and the microbes lose control of the temperature regulation, and temperature starts to follow β_{env}. We can see in Figure 4.9c that the system has not yet gone extinct at the end of the experiment, however it seems likely to do so.

When reducing β_{env} the system is now further from the microbes' preferred $\beta = 150$ than for the $\beta_{env} = 100$ experiments. This has the effect of making the low temperature limiting regime unviable earlier than before. The survival rate starts to drop off for lower τ.

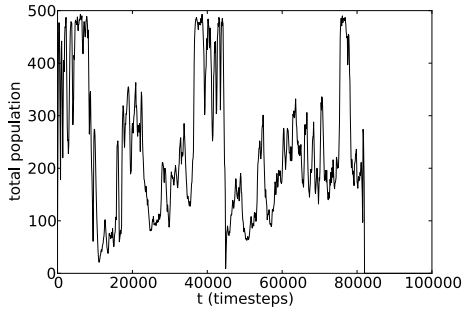
Figure 4.10 shows two $\tau = 0.015$ systems undergoing cooling. One system survives the experiment and one goes extinct. We can see that around roughly $80,000$ timesteps, β_{env} becomes too low to support the low temperature limiting regime. For a $\tau = 0.015$ system to survive therefore it must be in the high temperature limiting regime and remain there. Towards the



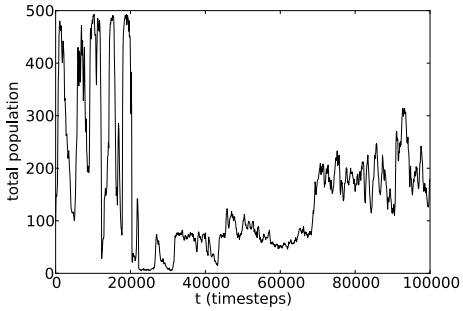
(A) $\tau = 0.015$ temperature plot.



(B) $\tau = 0.015$ temperature plot.



(C) $\tau = 0.015$ population plot.



(D) $\tau = 0.015$ population plot.

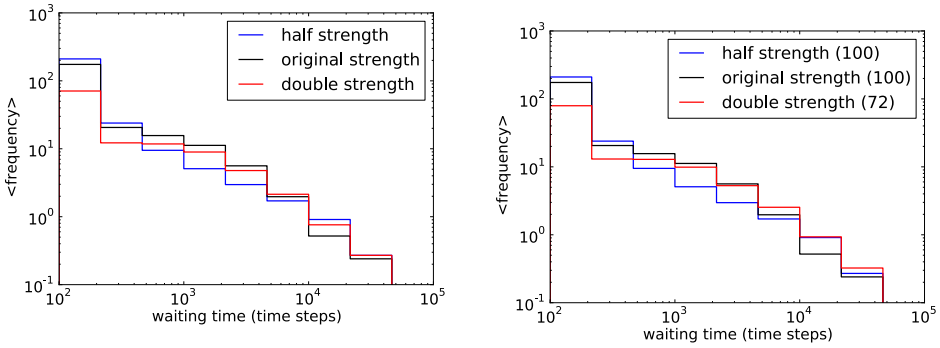
FIGURE 4.10: Cooling the system.

end of the cooling experiments we have a similar situation to the one we had for high τ when $\beta_{env} = 100$; the system must remain high temperature limited to survive, and quake events carry a high probability of total extinction, and these factors combine to reduce the survival probability for systems. Once β_{env} has fallen to below the temperature where low temperature limiting takes place T_L low temperature limitation becomes impossible. From Figures 4.10a and 4.10b we can see that $T_L \approx 70$.

If the system can remain in the high temperature limiting regime, then as β_{env} drops the microbes in the system can compensate by increasing their population and thus increasing their heating on the environment. We can see towards the end of Figure 4.10d that the population is increasing as β_{env} is dropping. If we decreased β_{env} enough, the microbes would reach a limit beyond which they would be unable to heat their environment sufficiently to reach the high temperature limiting regime. Beyond that point no form of temperature limitation is possible anymore and the temperature will fluctuate until the system is pushed to extinction, which given the extreme β_{env} would not take long.

3 .7 Changing the strength of the microbes' abiotic effects

The results so far have been for microbes with byproduct affects on the abiotic parameter generated from the range [-1, 1]. To investigate how the strength of these byproduct affects impact temperature regulation in the model, for $\tau = 0.015$ we preformed experiments with microbes with half-strength abiotic byproducts, i.e. taken from the range [-0.5, 0.5], denoted experiment S_H, and microbes with double strength abiotic byproducts, taken from the range [-2, 2], denoted experiment S_D. All 100 simulations survived for S_H, and 72 survived for S_D. Both systems showed temperature limitation, however S_H systems show more nutrient limitation than S_D systems. The frequency of waiting times for quakes was affected by changing the abiotic byproduct strengths as shown in Figure 4.11. The definition for a quake is the same as in Equation 4.4.



(A) Frequency of quakes for all simulations.

(B) Frequency of quakes for only non extinct simulations.

FIGURE 4.11: Histograms showing the average frequency of waiting times for quakes for $\tau = 0.015$ with different microbe byproduct strengths. The number of non-extinct simulations in b) is given in brackets in the legend. Note that both the x and y axis are logarithmic.

With weaker byproduct affects, the system can on average support a higher population of microbes while temperature limited, and this higher population means that there is a higher rate of mutants appearing in the system and thus a higher rate of destabilising mutants. We would then expect to see a higher frequency of quakes for S_H systems. From Figure 4.11 it does appear that S_H do not have to wait as long for quakes, as they have a higher frequency of quakes at small waiting times. For S_D systems we find the opposite, at small waiting times there is a lower frequency of quakes.

With stronger abiotic byproducts, on average there will be a smaller population supported during temperature limitation and thus a slower rate of mutants appearing, thus a smaller chance of destabilising mutants. S_D systems are also likely to become temperature limited faster than S_H systems as microbes have a stronger affect on the environment, it is easier for them to move the system away from nutrient limitation to temperature limitation, meaning that the system will spend less time with the temperature random walking during nutrient limitation, causing fewer rapid changes in temperature appearing in short time spans.

Otherwise the shapes of all three curves in Figure 4.11 are quite similar, demonstrating that changing the strength of the abiotic byproducts, although affecting the frequency of quakes for short waiting times, it does not have a large impact on the frequency of quakes for long waiting times.

We again have both a histogram from all experiments in Figure 4.11a and from only non extinct experiments Figure 4.11b. As S_D systems are the only systems to have any experiments go extinct, this is the only histogram that differs between the two, and we can see that for only non-extinct experiments, the frequency of quakes for longer waiting times is slightly higher than when we group extinct and non-extinct simulations all together.

3 .8 Changing P_{mut}

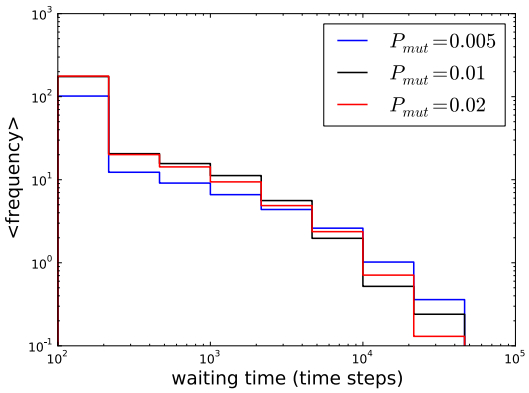


FIGURE 4.12: Histograms showing the average frequency of waiting times for quakes per non extinct simulation for $\tau = 0.015$ systems with different mutation rates. Note that both the x and y axis are logarithmic.

We investigated the effect of changing P_{mut} for $\tau = 0.015$ systems, and found that the qualitative dynamics of the system remained the same. The

survival rate for all systems was 100%. We found that a decreased rate of mutation $P_{mut} = 0.005$ resulted in fewer quakes at short waiting times, and more at longer waiting times showing the overall dynamics of the system to be slightly slowed down. Increasing the mutation rate to $P_{mut} = 0.02$ did not largely affect the expected waiting time for quakes. Figure 4.12 shows a histogram for the waiting times of quakes for each mutation rate. Importantly, temperature regulation was found to be present regardless of the value of P_{mut}.

4 Discussion

The single Flask model demonstrates environmental regulation arising from the byproducts of biota consistent with evolutionary theory, with a constant rate of mutation per reproduction event, and total extinction a possibility. Microbes in the model share a preference for the abiotic parameters but no spatial structure is present. This combination of assumptions differs from previous Gaian models demonstrating environmental regulation.

This model provides a quantitative illustration of more qualitative ideas from the late 1990's – that the most obvious way to make Gaian ideas compatible with evolutionary theory was for Gaian processes to be based on byproducts of processes that had been selected for other reasons (Volk, 1998; Wilkinson, 1999). A criticism of the Daisyworld model is that it is set up so that local adaptations of daisies in the system are also beneficial to global regulation. A black daisy is able to survive at a lower solar output than a white daisy due to its low albedo affect. It absorbs more energy thus heating its local environment and in turn the global environment pushing the Daisyworld towards habitability. As the solar output increases, white daisies start to take over to act in the reverse, cooling the planet. The daisies alter both the local and global temperature in the same direction meaning that what is selected for at the individual level directly impacts its global effects making Daisyworld a special case (Wood et al., 2008). The original multi-Flask model addressed this criticism by having the abiotic effects a byproduct rather than something to be selected for, as is the case in early Daisyworld models (Watson and Lovelock, 1983) and the Guild model (Downing and Zvirinsky, 1999), allowing environment improving local communities to develop and colonise and outcompete environment degrading communities leading to global regulation.

We have taken a step further in the single Flask model by having no local environment, only global. Any abiotic effect the microbes have acts on this global environment, and so a microbe is no more affected by the temperature increases / decreases due to its own metabolic processes than it is to the increases / decreases of others. This means all microbes feel the abiotic temperature identically at all times and none can gain an individual advantage due to its abiotic effects and competing communities cannot arise. Despite this, clear temperature regulation still appears in the system demonstrating that no spatial environment parameters are needed for temperature regulation to occur.

No single well adapted species emerges but the microbe ecosystem as a whole adjusts its total population to absorb the effects of mutants arising so that the total impact on the environmental parameter is kept constant. Internal perturbations arising from new mutants can knock the system from one temperature limiting regime to another and such transitions are rapid. In this way during temperature limitation we have a single negative feedback loop regulating the system, different from previous abiotic regulation mechanisms, such as the two 'rein' feedback in (McDonald-Gibson et al., 2008). As all microbes share a preference for the abiotic parameter, subgroups that pull the environment in different directions are not able to form. Instead, our single negative feedback mechanism can be thought of as a single 'rein' pulling against the abiotic parameter, with the strength of rein kept constant by a balance between ϵ_{avg} and the total population. The single rein can, for suitable τ pull in either direction to cause temperature limitation, with occasional regime shifts. Rapid regime shifts are a pattern also seen in nature (Wang et al., 2012). A real-world example of these large regime shifts is the evolution of oxygenic photosynthesis in the late Archean ultimately causing a transition from a reducing to an oxidising atmosphere (Catling, Zahnle, and McKay, 2001). However as there was more than a 300 Myr delay between the evolution of oxygenic photosynthesis and the rise in oxygen levels this real world example is more complex than the behaviour portrayed in this model.

Destabilising mutants – so called 'Ghengis Khan' species (Hamilton, 1995) – that greatly upset the current status quo, do not cause the system to go extinct for low and intermediate τ, rather they cause the system to quake and return to its previous temperature regulation, or can cause the system to flip from one temperature regulation to another. Dramatic change can take place in the system and yet the system can continue to exist. For high τ however, these 'Ghengis Khan' species can drive the system to extinction, as shown

by the low survival rate for $\tau > 0.015$. The rate of mutation in the model will determine how often these large scale destabilisations occur. Each time there is a mutation, the system will need to adjust to absorb the effects of the mutants metabolism. For a slower rate of mutation, the system would be more stable with large transitions occurring at longer intervals, and for a higher rate of mutation, the system would be destabilised more regularly.

We can think of the "regulator" of the system as being the total biomass production rate, rather than genetic distribution. The increase or decrease in the total biomass production rate, and in consequence the expansion and contraction of the total population is what regulates the temperature, while the genetic variation, determined by the reproduction and mutation rates, acts more like a perturbation the system must adapt to. In the event of a perturbation, the total biomass production rate required to maintain temperature regulation will change as ϵ_{avg} will now be different, and this will cause the actual total biomass production rate preformed by the system to change. The population will then increase or decrease until the average biomass production rate per microbe, reaches the replacement threshold, R_t, – the rate at which a stable population can be maintained, i.e. on average each microbe can reproduce once before its death. R_t is a constant throughout the simulation, so as the total biomass production rate changes as mutants are introduced, the population must adjust. There are no specific ecosystem engineers (Jones, Lawton, and Shachak, 1994) present in the model. There are no individual species that provide the regulation for other species to benefit from; all species collectively provide the temperature regulation. Some species may contribute towards regulation more than others at certain times, i.e. those with the largest population or the strongest abiotic affects per microbe, however we see from population and nutrient stock graphs that the genetic population of a ecosystem can be rapidly changing while temperature regulation continues uninterrupted. This model demonstrates how non-evolutionary mechanisms, i.e. feedbacks on growth (Lenton, 1998), can change the fitness landscape. In the multi-Flask world models, this mechanism would also be present, however the connected flasks allow for a higher-level selection to reduce the harmful perturbations of the 'wrong' kind of mutation, adding a second layer of regulation. 'Key-stone' species (Paine, 1969), species with a large effect on the environment per biomass, can occur and the death of such microbe's can also be a trigger for 'quakes'. If a microbe contributing strongly to the regulation dies, the regulation might be disrupted enough to allow for a transition to another regime.

The single-Flask model presents situations in which microbes sit in a nutrient-rich state but are unable to exploit them. With a nutrient rich environment we might expect the arrival of microbes able to exploit these abundant nutrients, however as it is the total biomass production that controls regulation in the temperature regulation state, all microbes will have their biomass production rates, and thus their reproduction rates, limited to the same value. In a shared environment, there is no way to select for a microbe that neutrally affects the current temperature value and thus can grow to a large population, exploiting the nutrients without affecting the temperature regulation. Even if the system could support a higher number of certain species and maintain regulation, there is no mechanism by which those species can reproduce at a faster rate, while ones that would destabilise the system do not. While it would be advantageous for the microbes to 'remove' their feedback on the environment, as it would remove extinction causing quake events, no organism can be independent of the physical environment, so the feedback will always exist. Life must take the resources it requires from the local environment and must dump its waste products into the environment (Wilkinson, 2006).

The first Flask model (Williams and Lenton, 2007) focused on syntrophy – cross-feeding or producer-consumer relationships, in a single flask. Robust nutrient recycling loops were found and we find this in our model too; if the microbe waste is removed immediately from the system after excretion, the total population of the system is reduced. The environment, however, in a single well mixed flask is the same for all microbes, and all resources are exchanged via the environment. Hence no 'exclusive' syntrophic relationships can emerge as any relationship is open to exploitation or parasitism and no multi-strain assemblages can be distinguished at a scale smaller than the single well-mixed flask.

The same system for a different value of τ can be nutrient limited or temperature limited. Natural systems can switch between nutrient limitation and some other abiotic environmental limitation, i.e. nutrient runoff from farmland into lakes leading to eutrophication – in this case the system goes from nutrient limited to some other limiting regime (Scheffer et al., 1993; Janssen et al., 2014), or potentially the response of some plants in the arctic tundra in response to warming where the plant may go from temperature limitation to nutrient limitation in areas of the High Arctic where nutrient levels are low (Walker et al., 2006). Therefore a model that can present both behaviours is useful although these smaller real-world examples are

not thought to be regulating their environments as strongly as this model demonstrates.

A longstanding argument against the Gaia hypothesis is that with just one Earth global regulation has no mechanism for developing because natural selection requires selection between multiple entities (Dawkins, 1982). This model shows that an ecosystem of 'temperature' sensitive microbes reacting in a simple way to changes in a global temperature can lead to robust temperature regulation. The system can be thought of as 'bouncing' off an upper or lower bound, similar to oxygen levels on Earth being upwardly bound by fire in the Phanerozoic (Lenton, 2001). This result weakens this criticism of the Gaia hypothesis. This temperature-regulation occurs only when the microbes are sensitive to the abiotic temperature. For regulation to occur there must be a feedback on the biota from the environment, without this, i.e. for low τ, the temperature cannot be regulated. When the microbes are sensitive to their environment however, temperature regulation robustly arises. For low to intermediate values of τ, systems have a high survival rate despite quakes upsetting the system. This suggests that for a range of τ between roughly $0 \leq \tau \leq 0.015$, we have what is known as a 'probable Gaia' (Lenton and Wilkinson, 2003). Systems tend towards stability with total extinction being a rare event. For higher values of around $\tau \geq 0.02$ we start to see extinctions becoming more probable; systems are less able to cope with quakes. The systems that survive do so due to the low number of quakes experienced during the experiment. In this scenario surviving systems are known as 'lucky Gaia' systems (Lenton and Wilkinson, 2003). Those that survive do so due to the low frequency quake inducing mutants arising.

The single Flask model has a number of limitations, the largest being that the abiotic effects by the microbes are a direct by-product of microbe metabolism. For each biomass created, a constant value determined by the microbes' genetics is added to the temperature. In the real world, direct heating effects from respiration have very little effect on parameters such as global temperatures. The effects come from the chemicals in the system, and these are influenced by life by what the life removes and provides to the system. In the example of global temperature, the concentrations of CO_2 and CH_4 are key in determining how insulating the Earth's atmosphere is. Another limitation is that the inflow and outflow rates providing and removing nutrients and abiotic parameters to the flask are rather rapid. This means that once a population of microbes slow or cease their metabolic activity, the abiotic parameters are quickly pulled back towards the equilibrium value,

the value it would have in the absence of life. This means that microbes do not have to suffer the consequences of destabilising mutants for too long and it enables the system to recover quickly – quickly here meaning a shorter length of time than the average lifespan of a microbe. The results of destabilising mutants are also almost immediately felt by the system allowing for rapid adaptation as soon as destabilising mutants arise. In many real world systems the feedback from a perturbation can take timescales that are much longer than the lifespan of the organisms creating the perturbation, for example the 300 Myr delay between the evolution of oxygenic photosynthesis and the Great Oxidation Event (Brocks et al., 1999). Therefore the effect of a destabilising mutant might take many generations to be felt preventing a rapid adjustment in the system before the mutant has left many descendants. This might prevent the system from successfully adapting to absorb perturbations of new mutants and might weaken the regulation mechanism. Another assumption the Flask model makes is that types of metabolism are not correlated with certain effects on the environment, for example heterotrophy and the production of CO_2, which warms the planet. In the Flask model the same metabolism can have different affects on the abiotic parameters depending on the genome of the microbe with that metabolism. This is more general than in the real world, and a limitation of the model.

We speculate that the identified regulation mechanism could in principle operate in natural well mixed environments, such as the Earth's atmosphere – i.e. regulation by fire near the upper bound for Oxygen (Lenton, 2001). Historically, massive regime shifts have occurred in global temperature and atmospheric composition without interrupting the existence of life on the planet. Our model shows similar patterns, and suggests a mechanism for how organisms might collectively interact via global parameters to regulate their environment.

A Single-Flask Model Description

A .1 The Flask Environment

We have a single well mixed environment with no spatial element – we assume that in the flask the liquid medium is well mixed so that the composition of the flask is in a homogeneous steady state. The flask is characterised by nutrient levels and the abiotic parameters. The nutrients present may be consumed by microbes and converted into biomass. The abiotic parameters are affected by and can affect the microbe activity.

The state of the flask is given by a vector V:

$$V = (n_1, ..., n_N, \beta^1_{env}, ..., \beta^A_{env}) = (v_1, ..., v_{N+A}) \tag{4.5}$$

where n_i is the concentration of nutrient i, β^i_{env}, is the level of abiotic parameter i, or equivalently, v_i, is the level of the i^{th} environmental state variable. N is the number of nutrients and A is the number of abiotic parameters.

As we break down each timestep into a number of iterations m where m is the total population of the system at the start of the timestep, we break down the inflow and outflow of nutrients and other abiotic parameters to prevent sudden changes at the the start of each timestep. The steps within a timestep would ideally all be computed in parallel but computational limitations prevent this, and so for agent based dynamics we effectively freeze the system while the selected microbes performs an action (being nutrient consumption / biomass production / reproduction / death). If we simply added and deducted the flow amounts at the start of each timestep, microbes selected at the beginning of a timestep could see a very different world to those selected at the end of a timestep if the population is large due to the microbes effect on the environment (nutrient consumption reducing nutrient levels and biomass creation affecting the abiotic parameters). Although these effects would largely average out due to the random selection of microbes during each timestep, a single large influx per timestep could be thought of as a periodic perturbation on the system which could affect the results seen. To counter this, we calculate the net influx of nutrients N^{net} and abiotic parameters at the start of each timestep:

$$N^{net} = I_N - O_N N^{current} \tag{4.6}$$

where I_N is the number of units of nutrient inflow per timestep, O_N is the percentage outflow, and $N^{current}$ is the current nutrient levels in the system

at the start of the timestep. We can then do $N^i = N^{net} / K^{current}$ where $K^{current}$ is the total population of the system at the start of the timestep, and then for each iteration within a timestep we increment the nutrient levels by N^i. This results in the same quantity of nutrients being added / removed from the system as if there was just one update at the start of the timestep, but it results in a much smoother transition and means that microbes selected at the start and end of a timestep will see much more similar worlds. In doing this, we treat nutrient levels as continuous but the microbes can only ever treat the nutrients as units. So while each iteration we might be adding 10.7 nutrient units per iteration, any microbes in the system can only act on the integer amounts of nutrients present.

We calculate the abiotic parameter changes by diluting the current abiotic parameters by a certain percentage of fresh influx I_A. So for the abiotic parameters we update each iteration by A^{net}:

$$A^{net} = A^{source} I_A - A^{current} I_A \tag{4.7}$$

where A^{source} is the abiotic parameters of the source, and $A^{current}$ is the abiotic parameters of the current environment in the flask.

A .2 Microbes

The microbes consume and excrete nutrients in fixed proportions and affect the levels of abiotic parameters in their environment as a side effect of biomass creation. The ratios of nutrient consumption / excretion and the byproduct effect on the abiotic parameters are genetically encoded for each microbe species. All microbes share the same preferred abiotic conditions (i.e. the state of the abiotic environment which results in the maximum growth rate). Microbes grow by consuming nutrients and converting them to biomass, and they reproduce asexually by splitting once their biomass reaches a threshold. Biomass is reduced by a fixed amount per timestep to represent the cost of staying alive. Microbes die if their biomass drops to a fixed threshold, which can happen during nutrient limitation or temperature limitation causing the microbes being unable to consume the nutrients present.

In the code we do not record microbes of the same species individually as doing so would slow the code considerably. Instead we group microbes of the same species together and record the species' total biomass. Thus each species can be thought of as a vector S:

$$S = (G, K_S, B, \lambda, \mu, \alpha, \beta) \tag{4.8}$$

where G is the species' genome (represented as a decimal number), K_S is the population of the species, B is the total biomass of the species. $\lambda = (1, ..., N)$ represents the ratio in which nutrients are consumed (e.g. for $N = 4$ we could have $\lambda = (0, \frac{1}{3}, 0, \frac{2}{3})$), $\mu = (1, ..., N)$ represents the ratio in which excreta are returned to the environment as nutrients, $\alpha = (1, ..., A)$ represents the effect from one microbe in the species on each abiotic parameter, and $\beta = (1, ..., A)$ represents the environmental abiotic parameter levels that maximise the growth for microbes in species S.

A .3 Genotype

The genotype of a microbe is recorded as the decimal representation of an 8 bit binary string, and this is used to group microbes into species. Microbes that share the same genome are of the same species. We create tables for microbe nutrient / excretion rules and abiotic effects and this genome is used as the reference to look up the particular metabolism rules for a microbe. With an 8 bit long binary genome there are 256 possible species (as each 'gene' in a genome can have the value 0 or 1).

A .4 Reproduction and Mutation

If the microbe is able to consume enough nutrients to reach the reproduction threshold T_R it will reproduce asexually, splitting in half. Half of the biomass with go to the new microbe and the parent microbe will half its biomass. The new microbe will have the same genome as the parent unless a mutation occurred during the reproduction. There is a small constant probability of mutation for each locus. If a mutation occurs at a locus then the 'gene' at that point will be 'flipped', turning it to 0 if it were previously 1, or to 1 if it were previously 0.

A .5 Maintenance Cost and Death

There is a fixed biomass cost of staying alive for each microbe. This reduces a microbe's biomass by a constant rate. This cost represents the energy costs of maintaining cellular machinery and metabolic inefficiency. This cost is assumed to be lost from the flask environment as unrecoverable heat radiation. This ensures that the nutrients cannot be infinitely recycled and it sets the

carrying capacity of the system. This carry capacity is reached when the total heat dissipation matches the energy supplied in the form of nutrients.

If the biomass falls to a starvation threshold T_D the microbe will starve to death. There is also a small probability of death by natural causes P_D that represents death by predation, apoptosis etc. When a microbe dies its biomass is be removed from the system, as if the dead microbe were washed out of the flask.

A .6 Nutrient Consumption / Excretion

During a single timestep a different microbe is selected n times for a nutrient consumption event, where n is the total population of the system at the start of the timestep. This means that on average every microbe will be selected for nutrient consumption once per timestep. When a microbe is selected it will attempt to eat its C_j^{max} of nutrients (the value of C_j^{max} depending on how closely the abiotic parameters meet the microbes' preferred values and the microbes' sensitivity to its environment), and if the nutrients are available, and in the correct ratios, the microbe will consume them. The nutrient ratios are fixed at the start of each simulation for each genome and remain constant.

The nutrient consumption / excretion vectors for each genome are of N length, where N is the number of nutrients. If we assume we have 3 nutrients we would then have 2 vectors of length 3. We populate these vectors with random numbers generated between $[-1, 1]$ and then sum. For example if our two vectors were $[-0.3, 0.5, 0.6]$ and $[-0.2, -0.2, 0.1]$ then summed we would have: $[-0.5, 0.3, 0.7]$. We take negative values to mean that nutrient is excreted and positive values that that nutrient is consumed. Therefore any case where all values in the vector are positive or all are negative are instantly disqualified as a microbe must eat and excrete. For our example above we see that our microbe consumes nutrients 2 and 3 and excretes nutrient 1. When consuming nutrients this microbe must eat 3 units of nutrient 2 with 7 nutrients of nutrient 3 (a unit of nutrient is non divisible), or the microbe cannot consume anything. This particular metabolism is limiting the microbe to be only able to survive in ideal abiotic conditions, if we take our $C^{max} = 10$ (the maximum consumption rate for any microbe) as if the abiotic conditions move away, we get $C_j^{max} < C^{max}$ and so $C_j^{max} < 10$ and with our specific nutrient ratio, if the microbe cannot eat 10 units of nutrient, it cannot consume at all or it would violate its metabolic nutrient ratio rules.

A .7 Effect of abiotic factor on metabolic rate

The state of the abiotic environment affects the rate at which microbes can consume nutrients which in turn affects the rate of biomass production and thus the growth of the microbes. A microbe will attempt to consume a maximum amount C_j^{max} of nutrients each timestep with the demand being met depending on nutrient availability. The C_j^{max} is calculated for each microbe j as a function of the match between the microbes' genetically specified preferred conditions and the current abiotic state of the environment. This function is has a Gaussian form and falls away smoothly from its maximum as the distance between the optimum and the current environment increases. Mathematically we write this as:

$$C_j^{max} = \psi_j C^{max} \tag{4.9}$$

$$\psi_j = e^{-(\tau p_j)^2} \tag{4.10}$$

$$p_j = \sqrt{\sum_{i=1}^{A} (\beta_{env}^i - \beta_j^i)^2} \tag{4.11}$$

where C_{max} is a constant determining the maximum rate of consumption for any microbe, ψ_j is a microbe specific measure of the microbe's satisfaction with the current abiotic environment, τ is a universal constant parameter that determines how sensitive the microbes are to their environment ($\tau = 0$ means the microbes are not affected by the abiotic environment at all, and a higher τ means the microbes become more sensitive to the abiotic conditions). p_j is a measure of the distance between the current environmental level for each abiotic factor β_{env}^i and the microbe's preferred level β_j^i.

A .8 Effect of microbial activity on environment

Microbes can affect their abiotic environment as a side effect of biomass creation. The effect the microbe has is proportional to its rate of biomass creation and thus its growth rate, so faster growing species will have a larger effect than slower growing species. Through the consumption of nutrients and excretion of waste products microbes also affect the nutrient levels in the environment.

Each microbe has an effect on the abiotic parameters per unit of biomass created, and these effects are numbers in the range $[-1, 1]$. These numbers

are randomly generated in this range at the beginning of each simulation for each species and remains constant throughout the simulation. Thus each member of a species has the same effect on the abiotic environment for the duration of the simulation.

A .9 Parameters

The model parameters used to generate the data presented in this work are found in Table 4.3.

A .10 Method

We used agent based dynamics to run the simulation. A timestep is broken down into iterations, the number of iterations matches n the number of microbes alive in the system at the start of the timestep. For each iteration we perform the following steps:

- Influx / outflux of abiotic parameters and nutrients via trickle
- An individual selected randomly for a death event
- An individual selected randomly for a nutrient consumption event
- An individual selected randomly for a biomass creation event
- An individual selected randomly for a reproduction event

We repeated this process n times for one timestep.
Each simulation in this paper was run for 10^5 timesteps.

TABLE 4.3: Model parameters

Parameter	Value	Description
N	4	Number of nutrients
A	1	Number of abiotic parameters
B_R	120	Reproduction threshold (biomass units)
B_D	50	Starvation threshold (biomass units)
P_{mut}	0.01	Probability of mutation at each locus during reproduction
P_D	0.002	Probability of death by natural causes (other than starvation) at each timestep
λ	1	Maintenance cost (biomass units / timestep)
θ	0.6	Nutrient conversion efficiency
C^{max}	10	Maximum number of nutrients a microbe can consume in any single event
τ	[0.00, 0.005, 0.01, 0.015, 0.02, 0.025, 0.03]	Level of influence of abiotic environment on metabolism
I_N	150	Rate of nutrient influx (units / timestep)
O_N	0.25	Rate of nutrient outflux (percentage / timestep)
I_A	0.2	Rate of abiotic factor influx (percentage / timestep)
O_A	0.2	Rate of abiotic factor outflux (percentage / timestep)
K_M	100	Number of individuals in flask inoculum
t_{prep}	500	Flask equilibration time prior to seeding (timesteps)
t_{run}	10^5	Duration of run (timesteps)
β	150	Abiotic environmental preference
β_{env}	100	Environmental 'temperature' in the absence of microbe activity

Chapter Summary

This chapter has explored the single-flask model and the regulation mechanism that emerges within it. I have demonstrated how a microbe community living within a single shared global environment can act to regulate global parameters, temperature being the example given, via single-rein control. Within the model microbes impact the global temperature via their metabolisms – adding an amount to this temperature per biomass created, with this amount determined in their genetic code. In single-reign control two temperature limiting regimes emerge at symmetric distances either side of the microbes 'ideal' temperature – where their fitness is as a maximum. These temperature limiting values are where the birth rate of the microbes matched the death rate, i.e. a stable population is achieved. However the microbe community is constantly changing as new mutants emerge or old members of the community die, and this will cause the communities impact on the environment to change. To maintain the temperature at either of these limits the total population of the microbe community is constantly responding and adapting to changes within the microbe community in order to maintain a near constant biotic impact on the environment. As the average impact of a microbe on the environment changes, as new mutants emerge or old members of the community die, the population responds, either increasing or decreasing, until the overall impact of life on the environment is again at the regulation point.

In the single-flask model, the microbe communities are self-limiting towards degrading their environment – if they push their world towards uninhabitability, their impact on their environment decreases and abiotic processes will dominate, moving the environment back towards habitable ranges. In this way so called 'anti-Gaias' are not typical in single-flask worlds. When life is very sensitive to the environmental temperature it can result in the system only being able to support low populations at one of the temperature limiting regimes, which does make the system more prone to extinction causing fluctuations. However in the single-flask model the dominating behaviour is that of regulation and long term persistence of life.

Chapter 5

Alternative Mechanisms for Gaia

With the single-flask model I explored in detail the regulation mechanism of single-rein control. In this chapter, I explore how selection mechanisms can influence the likelihood of systems surviving long enough to develop such regulation mechanisms. There is a probabilistic element to forming a Gaian system. All the ingredients might be present, and yet self-regulation might fail to establish itself. It is therefore also important to investigate selection mechanisms for Gaian systems to understand how probable a habitable Earth was.

This chapter presents a model designed to explore a hypothesis laid out in Doolittle (2014) of “Selection by Survival". The thought experiment suggests that planets that have hosted life for longer have a higher chance of having acquired self-regulatory feedbacks, and so the longer a life-planet coupled system persists, the greater its probability of future persistence. In the following work a flask model variant shows that the strength of the effect of selection by survival for various scenarios of self-regulatory properties.

The work presented in this chapter was published in the Journal of Theoretical Biology, November 2018, titled “Alternative Mechanisms for Gaia” (Nicholson et al., 2018). The initial concept for creating a model to explore selection by survival came from my supervisor Dave Wilkinson and I adapted the single-flask model (Chapter 4) to explore this hypothesis. I was the lead author on this paper. My contributions include writing the code to generate the data presented, analysing the data, and creating the graphs figures, and I wrote a significant portion of the manuscript. The work is presented as its published form, only differing in the correction of a few typos found since publication and has been taken out of the journal formatting.

Alternative Mechanisms for Gaia

Arwen E. Nicholson, David M. Wilkinson, Hywel T.P. Williams and Timothy M. Lenton

Abstract

A long-standing objection to the Gaia hypothesis has been a perceived lack of plausible mechanisms by which life on Earth could come to regulate its abiotic environment. A null hypothesis is survival by pure chance, by which any appearance of regulation on Earth is illusory and the persistence of life simply reflects the weak anthropic principle – it must have occurred for intelligent observers to ask the question. Recent work has proposed that persistence alone increases the chance that a biosphere will acquire further persistence-enhancing properties. Here we use a simple quantitative model to show that such 'selection by survival alone' can indeed increase the probability that a biosphere will persist in the future, relative to a baseline of pure chance. Adding environmental feedback to this model shows either an increased or decreased survival probability depending on the initial conditions. Feedback can hinder early life becoming established if initial conditions are poor, but feedback can also prevent systems from diverging too far from optimum environmental conditions and thus increase survival rates. The outstanding question remains the relative importance of each mechanism for the historical and continued persistence of life on Earth.

1 Introduction

The Gaia hypothesis postulates that life on Earth forms part of a self-regulating planetary-scale system with stabilising properties that help to maintain habitable conditions (Margulis and Lovelock, 1974; Lovelock, 1979). Early critiques of Gaia by evolutionary biologists questioned the compatibility of Gaia with natural selection (Doolittle, 1981; Dawkins, 1982) and noted that an appeal to the weak anthropic principle could account for the long persistence of life on Earth without requiring regulatory mechanisms (Doolittle, 1981). Subsequent proposals that global environmental feedbacks could be built on by-products of metabolic traits selected for more proximate ecological benefits sidestepped this evolutionary critique, but raised the question of

why stable outcomes would be any more likely than unstable ones (Lenton, 1998; Volk, 1998; Wilkinson, 1999). A series of theoretical models of feedback between life and the environment then showed that self-stabilising outcomes can arise from metabolic by-products in a manner consistent with natural selection (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010) and possible selection mechanisms for Gaia have been identified across multiple scales (Lenton et al., 2018).

Recently, a new schematic model of 'selection by survival' alone has been proposed (Doolittle, 2014), whereby postulated biospheres can acquire persistence-enhancing adaptations by chance over time. In the language of this model, macro-level 'mutations' affecting biosphere dynamics and stability arise due to micro-level mutations that occur during reproduction of the organisms that compose the system. Thus the longer the biosphere persists, the greater the likelihood that persistence-enhancing mutations can arise. This could apply to the Earth's biosphere as well as smaller entities such as ecosystems (see (Toman and Flegr, 2017) for a wider discussion of such approaches). Here we introduce a quantitative model of this idea and contrast it with a null model of survival by pure chance, and then investigate the effect of adding feedback using an existing model of environmental feedbacks.

2 Model

We compare three hypotheses for the continued persistence of life on Earth:

H1 - Null hypothesis (pure chance)

H2 - Acquisition of persistence enhancing mutations by chance (selection by survival)

H3 - Environmental feedbacks in addition to selection by survival.

In an attempt to isolate the effect of life on its own persistence we use idealised model biospheres where the abiotic environment is highly simplified and where the biosphere has a non-zero likelihood of extinction which can be impacted by the biosphere. For each scenario, we consider a non-interacting population of 10^4 isolated model biospheres and consider how many survive as a function of time. Appendix A contains a full model description. The models used in each scenario are described below.

2 .1 H1 – Null Hypothesis

For the null model we assume a constant extinction probability for each biosphere at each model timestep, resulting in exponential decay in the number of surviving biospheres. The probability of extinction at any time for H1 systems is a constant:

$$P_C = C \tag{5.1}$$

We set C to have the same value as the starting extinction values for the selection by survival (H2), and the environmental feedback (H3) experiments. This allows us to identify any survival enhancement performed by the biospheres in these experiments.

2 .2 H2 – Selection by Survival

For the selection by survival (Doolittle, 2014) experiment we adapt a pre-existing model – the Flask model (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010; Nicholson et al., 2017). This consists of model 'flasks', host to microbe communities (these could be thought of as effectively chemostats – at the small scale – to whole biospheres, at a large scale). These flasks experience inflow and outflow of a medium containing nutrients. Microbes consume nutrients, produce waste, and impact the abiotic environment (here represented as a single variable arbitrarily labelled 'temperature', T) as a by-product of their metabolic activity. The flask inflow medium is at a constant temperature T_{inflow}. Microbes starve to death if their biomass drops below a certain threshold B_D and reproduce asexually if their biomass reaches the reproduction threshold B_R. During reproduction mutations can occur leading to new species emerging. There is also a constant probability of random mortality of microbes D. There are 4 nutrient types in each system, and microbes can consume and excrete a combination of any, however every microbe must both consume and excrete, and it must not consume what it excretes, otherwise it is unviable. The pattern of consumption / excretion is set by the microbe's genotype, which can mutate at reproduction.

For our selection by survival experiments, we limit the system to a single flask; we can think of these flasks as self-contained planets host to biospheres. Microbial metabolisms impact the system temperature, but this temperature does not impact individual microbes' metabolisms. The temperature does impact the biosphere-wide probability of extinction P_T:

$$P_T = a + b \times |T_{ideal} - T| \tag{5.2}$$

where T is the system temperature, and depends on the genetic makeup of the microbe community currently alive in the system, $a = 2 \times 10^{-6}$ is a constant background probability of global extinction, and $b = 2 \times 10^{-6}$ controls the impact the system temperature has on the probability of extinction. Here there is a global T_{ideal} value, which is the system temperature that results in the lowest probability of total extinction. The inflow to the system is at temperature $T_{inflow} \ll T_{ideal}$. This makes initial conditions far from ideal, however still tolerable to the temperature sensitive H3 microbes, thus allowing for direct comparison. We seed with a single microbe species set to have no impact on the system temperature. As mutants arise, they will affect system temperatures via their metabolisms, but for each experiment the environment starts with the same conditions. This allows us to see the effect the selection by survival mechanism has more clearly. The selection by survival model is very similar to the version of Flask model detailed in (Nicholson et al., 2017) however with the feedback from environment to microbe metabolisms removed, and the temperature dependant P_T – the biosphere-level mortality process – imposed on each system.

2 .3 H3 – Adding Environmental Feedbacks

The environmental feedback case (H3) is similar to the selection by survival model (H2) with the key difference that the temperature does now impact individual microbes' growth rates. H2 systems have feedback acting in one direction only, from the microbes to the environment. H3 systems have the same life $\rightarrow$ environment interaction, but also feedback from the environment to the microbes, thus closing the feedback loop.

For H3 systems, microbes are temperature sensitive with their growth rate impacted by the system temperature. The growth rates for all microbes are at a maximum when $T = T_{ideal}$, i.e. T_{ideal} is the temperature at which their metabolic activity will be at its peak. As the system temperature moves away from T_{ideal}, microbe metabolic activity slows until eventually they cannot consume nutrients at all. If conditions do not quickly improve, the result is individual mortality of microbes which can lead to extinction. This model is the Flask model described in (Nicholson et al., 2017), however with the biosphere-level mortality function P_T (Equation 5.2) imposed on each system. The microbes' temperature sensitivity is determined by a parameter τ

that takes a real positive value, and is the same for all species (earlier work e.g. (Williams and Lenton, 2010) explores scenarios where τ differs between species). A higher τ value corresponds to more temperature sensitive microbes. The fitness F of the microbes depends on τ in the following way:

$$F = e^{-(\tau|T_{ideal}-T|)^2} \tag{5.3}$$

Setting $\tau = 0$ would give a system of microbes that are completely temperature insensitive with $F = 1$ for all temperatures, i.e. H2 systems. When $\tau > 0$, the microbes' fitness is a Gaussian function, centred around $T = T_{ideal}$, and as $\tau \to \infty$, the fitness function becomes a delta function, with a non-zero value for only $T = T_{ideal}$. When the microbes metabolisms are at a maximum, the system will also have the lowest P_T value (as determined by Equation 5.2). For H3 systems, microbes now feel the effects of an improving or a degrading environment and their metabolic activity will be impacted – this in turn will impact the system temperature resulting in a feedback loop.

Figure 5.1 shows a schematic of an H2 / H3 system. It is these systems that are subject to the P_T extinction values, and the microbial actions happening inside each system determine the value of P_T.

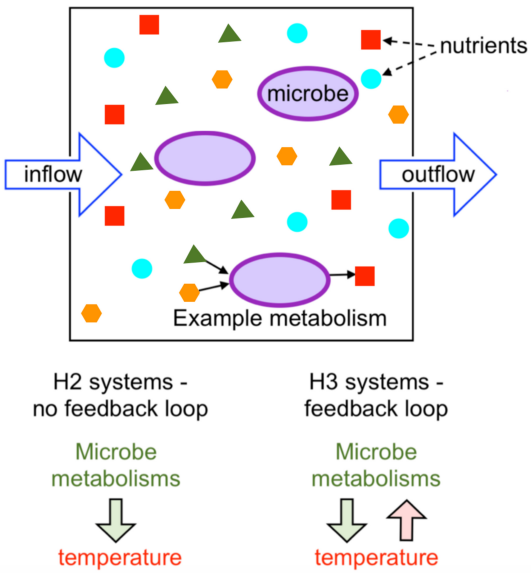


FIGURE 5.1: Schematic of an H2 or H3 system, showing the nutrient medium (with inflow and outflow), the microbes, and an example microbe metabolism. For H2 systems, microbe metabolisms impact the system temperature, but are temperature independent themselves. In H3 systems, microbe metabolisms impact the system temperature and are temperature sensitive, resulting in a feedback loop.

3 Method

We start the experiment with each model system with a temperature that does not match the microbes 'ideal' temperature (i.e. with $T_0 \neq T_{ideal}$) to test the model's ability to approach ideal conditions. All H1, H2, and H3 systems begin each experiment with the same system temperature, T_0, and we set $P_C = P_{T,0} = a + b \times |T_{ideal} - T_0|$. The value of T_0 will be the temperature of the medium inflowing to each system, T_{inflow}. We set $T_{inflow} = 0$, and therefore $T_0 = 0$, for all experiments. For all experiments, the parameters a and b in Equation 5.2 have the values $a = b = 2 \times 10^{-6}$. The values of P_C vary as T_{ideal} varies between experiments and we have $P_C = \{10.02 \times 10^{-4}, 6.02 \times 10^{-4}, 2.02 \times 10^{-4}\}$ for the corresponding values of $T_{ideal} = \{500, 300, 100\}$.

H2 and H3 systems are seeded with a single microbe species with a metabolism that has zero impact on the system temperature. When mutants emerge, their metabolisms may impact the temperature. We perform 10^4 experiments with different random initialisations for each hypothesis in order to robustly observe the system behaviours exhibited in each scenario.

To test the H2 hypothesis we perform 3 sets of experiments for systems with $T_{ideal} \in \{500, 300, 100\}$. To then test how H3 systems compare to H2, we perform, for each T_{ideal} case, 3 further studies with differing τ strengths to investigate how changing the microbes' sensitivity impacts model results. For $T_{ideal} = 500$ we perform H3 experiments with $\tau \in \{0.002, 0.0025, 0.003\}$, for $T_{ideal} = 300$ we investigate $\tau \in \{0.003, 0.004, 0.005\}$, and for $T_{ideal} = 100$, our H3 experiments are $\tau \in \{0.005, 0.007, 0.009\}$. This allows us to explore how these key parameters impact the system behaviours. The starting τ value for each T_{ideal} set of experiments corresponds to the end τ for the previous set. I.e. the last τ explored for $T_{ideal} = 500$ is $\tau = 0.003$ and thus the first τ explored for $T_{ideal} = 300$ is also $\tau = 0.003$. This allows us to see how shifting T_{ideal} while keeping τ constant affects the H3 systems while still enabling us to explore a suitable τ range for each T_{ideal}. An in-depth exploration of how various system parameters impact the Flask model can be found in (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010; Nicholson et al., 2017).

4 Results

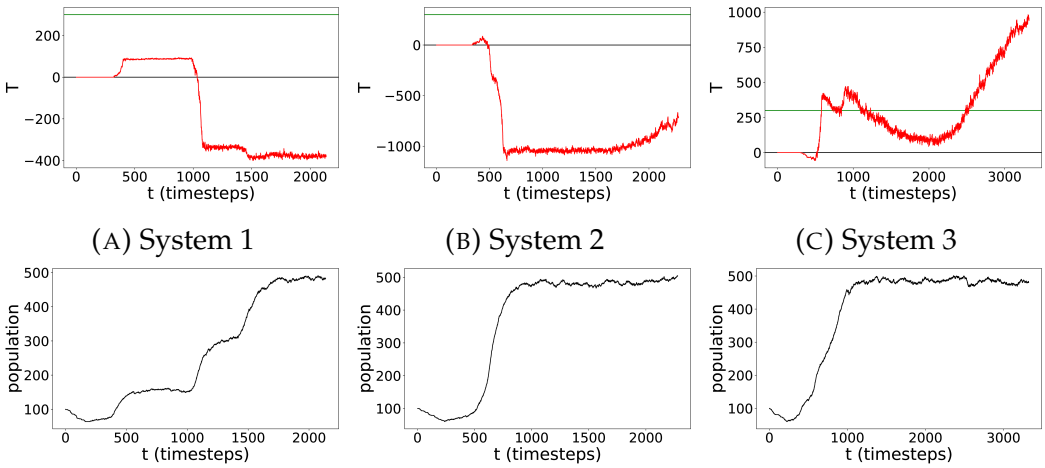
How the H2 and H3 experiments perform, compared to each other and compared to the null, is strongly dependent on how closely the initial conditions match the microbes' preferred conditions, i.e. how large the value of $|T_{ideal} - T_0|$ is, and for H3 systems, how sensitive the microbes are to their environment. This is summarised in Figure 5.5, which shows a series of experiments with varying T_{ideal} values and microbe sensitivities τ (with $T_0 = 0$ for each case). These figures show the number of surviving systems over time for the null H1 systems, selection by survival H2 systems, and environmental feedback H3 systems. Each figure also includes the 'Ideal' survival probability i.e. for $|T_{ideal} - T| = 0$ for all time. The 'Ideal' case is included as a 'perfect world' baseline for comparison. We return to this part of the analysis later, after first considering the behaviours of the H1, H2, and H3 systems.

4 .1 H2 systems (selection by survival)

We first examined individual H2 systems to determine their typical characteristics. H2 systems are not temperature sensitive and so the only limiting factor on the total population size is nutrient availability. Once the population has reached the carrying capacity of the environment (i.e. consuming all available nutrients) the population will remain stable there, regardless of the system temperature. The system temperature will change as the microbe community changes; as new mutants emerge, species die, and the relative populations of existing species shift, the temperature will perform a 'random walk' and change in an unguided manner.

Figure 5.2 shows the trajectories of the system temperature (with T_0 shown in black and T_{ideal} shown in green) and the total population for 3 individual runs. System 1 (Figures 5.2a and 5.2d) shows several abrupt temperature changes happening in the system, and these correspond with jumps in the total population, shown in Figure 5.2d. Each system is seeded with a single microbe species that consumes only 1 nutrient source, therefore at the beginning of each experiment, there are 3 unexploited sources of food (as there are 4 nutrient types in total). If a mutant emerges that consumes a currently abundant nutrient, its population can rapidly increase due to the abundance of food, causing rapid temperature changes due to the metabolic byproducts of this new mutant. Once all nutrients are exploited, new mutants emerging

have no advantage over existing species and so temperature changes can remain relatively stable over long time periods. In System 2 (Figures 5.2b and 5.2e), once the carrying capacity is reached, the system temperature remains relatively stable at around $T \approx -1000$ (which is very far from $T_{ideal} = 300$). In contrast, System 3's temperature (Figure 5.2c) slowly changes over the course of the experiment. System 3 quickly reaches the carrying capacity (Figure 5.2f) and then as the microbe community changes over time, the temperature changes. For H2 systems, once microbes have evolved to consume all available nutrients the population remains near constant. Sustained decreases in the population size are highly unlikely.



(A) System 1 (B) System 2 (C) System 3

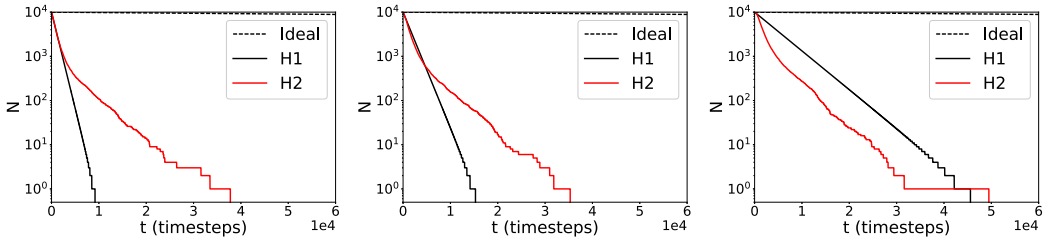
(D) System 1 (E) System 2 (F) System 3

FIGURE 5.2: Temperature (T) vs time and total population vs time for individual H2 systems with $T_{ideal} = 300$. In the temperature plots T_0 is shown as a black horizontal line, and T_{ideal} is shown in green.

To test whether selection by survival is a viable mechanism, we first examine the H2 systems and compare them to the null H1 systems. Figure 5.3 shows the surviving number of H2 biospheres (red lines) and H1 biospheres (black solid lines) over time, where $T_{ideal} \in \{500, 300, 100\}$ respectively (note the log-scale y-axis). Figure 5.3a shows the results for the experiments where $T_{ideal} = 500$ and initial conditions are far from T_{ideal} ($T_0 = 0$). Initially the H2 and H1 systems die out at a similar rate, but after this initial period the H2 systems begin to show improved persistence relative to the H1 systems, and a significant number of H2 biospheres go on to live for much longer timespans than the longest lived H1 system.

For H1 systems, the biosphere does not impact the system temperature, T, and therefore P_C, is constant for all time. In H2 systems, microbes are changing their environment as they metabolise nutrients and this can either

increase or decrease their survival probability. For those that degrade their environment, their P_T value will be higher than the P_C value, and hence these degrading systems tend to go extinct faster. However, those that improve their environment experience lower P_T values and so can experience much longer lifespans.



(A) $T_{ideal} = 500$ (B) $T_{ideal} = 300$ (C) $T_{ideal} = 100$

FIGURE 5.3: Number of surviving biospheres (N) against time. Selection by survival systems (H2) shown in red, and null hypothesis (H1) in black. Note the log-scale y-axis.

Figures 5.3b and 5.3c show that as T_{ideal} comes closer to T_0, the positive impact of selection by survival decreases, until H2 systems suffer on average poorer survival rates than H1 systems. Each H2 biosphere is effectively a randomly walking system, with the impact from the microbes on the environment changing as the microbe community changes over time due to death, reproduction and mutation. When initial conditions are far from ideal, there are a large number of possible random walks that will improve the environment and thus improve survival odds. As the distance between T_{ideal} and T_0 closes, the number of random walks that are environment improving decreases, until, for conditions where $T_{ideal} = T_0$, any alteration of the environment by the microbes decreases survival probabilities. The case where $T_{ideal} = T_0 = T$ for all time is shown in each figure as the 'Ideal' case. Therefore the mechanism of selection by survival sees the best improvement in biosphere survival probability when initial conditions are poor for life.

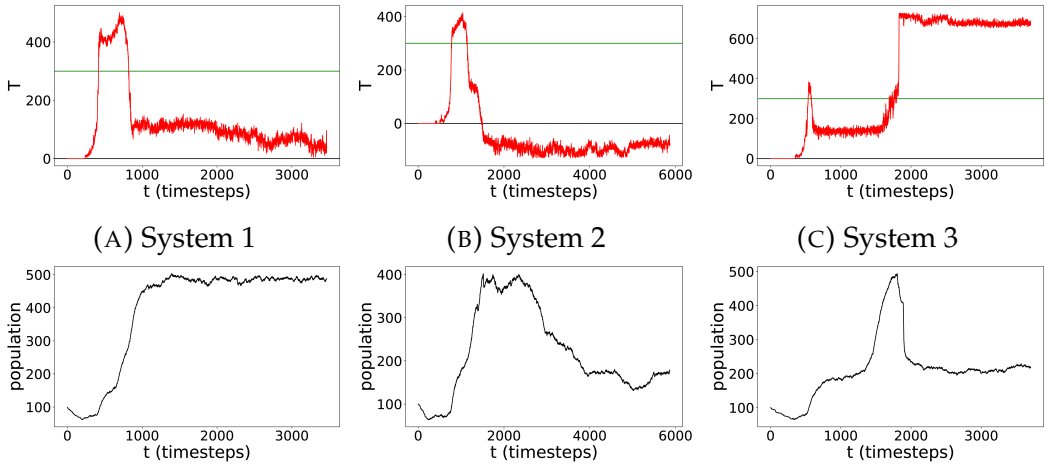
Although the relative success between H1 and H2 systems is impacted by changing T_{ideal}, the H2 survival rates in Figures 5.3a - 5.3c are similar – the distance between T_{ideal} and T_0 does not greatly impact the selection by survival mechanism. For different T_{ideal}, H2 systems start with different $P_{T,0}$ values, however as H2 biospheres rapidly move the system temperature away from T_0 and keep it under their control, the starting proximity to ideal environmental conditions ceases to matter. For H1 systems where $T = T_0$ for all time, the distance between T_{ideal} and T_0 has a large impact on survival rates.

4 .2 H3 systems (environmental feedback)

H3 microbes, in constrast to H2 microbes, are temperature sensitive and so changes in the system temperature impact their metabolisms. Figure 5.4 shows the temperature and total population for the individual trajectories of 3 H3 systems, with T_0 shown in black and T_{ideal} in green. Some H3 systems behave similarly to H2 systems, with the total population quickly reaching the carrying capacity, and the temperature slowly changing as the microbe community changes, e.g. System 1 (Figures 5.4a and 5.4d). For systems where the temperature wanders towards the bounds of habitability, H3 systems behave differently. The temperatures in both Systems 2 and 3 (Figures 5.4b and 5.4c) wander far from T_{ideal} and then remain at a near constant temperature. In System 2, while the temperature remains near constant, the population changes over time (Figure 5.4e), and in System 3, the population remains at a near stable population lower than the carrying capacity, and lower than previous populations experienced by the system (Figure 5.4f). In these cases the H3 systems enter temperature limiting regimes, with System 2 entering the lower temperature limiting regime at $T = T^-_{lim} \approx -100$ at $t \approx 1900$ and System 3 entering the high temperature limiting regime, with $T = T^+_{lim} \approx 700$, at $t \approx 2000$.

These temperature limiting regimes are characterised by a near stable temperature maintained by a negative feedback loop, with the total impact of the biosphere on the environment 'pulling' the system temperature one way, and the inflow medium at $T = T_0$ 'pulling' the temperature in the opposite direction. This is known as 'single rein-control' (Nicholson et al., 2017). For a system to be at $T = T^+_{lim}$ the biosphere must be overall heating, and similarly for $T = T^-_{lim}$ the biosphere must be overall cooling. At $T = T^{+/-}_{lim}$ if the environment degrades, the total population reduces as microbe metabolisms suffer, and this reduces the cause of the environmental degradation (microbe metabolic byproducts) allowing the inflow medium to bring temperatures back towards T_0 thus improving habitability. If at $T^{+/-}_{lim}$, the environment improves, microbes will proliferate, increasing their impact on their environment and pushing temperatures back towards $T = T^{+/-}_{lim}$. This leads to temperature regulation, which can be exited via a positive feedback (microbes causing environment improvement and leading to greater populations) until either the alternate temperature limiting regime is reached, or the system becomes nutrient limited. System 2 (Figure 5.4e) clearly shows the microbe population adjusting in response to microbe community changes while a near constant temperature is maintained (Figure 5.4b).

The values of T^{+}_{lim} and T^{-}_{lim} will depend on τ and T_{ideal}. A higher τ will result in a smaller distance between T_{ideal} and $T^{+/-}_{lim}$. Examining Figure 5.4b we can see that for a strong enough τ, $T^{-}_{lim} > T_0$ would be true. If this were the case, the initial microbe population would be unable to survive its environment and would quickly go extinct. If $T^{-}_{lim} \approx T_0$, then the early environment will only be able to support a very small cooling biosphere which would be more prone to extinction due to stochastic fluctuations. Biospheres with high τ will also have a narrower window of temperatures where the system is nutrient limited and so these systems will be more likely to become temperature limited and become 'stuck' at these $T^{+/-}_{lim}$ values, which would prevent the temperature from reaching values closer to T_{ideal} and thus prevent the corresponding low P_T values for H3 systems.



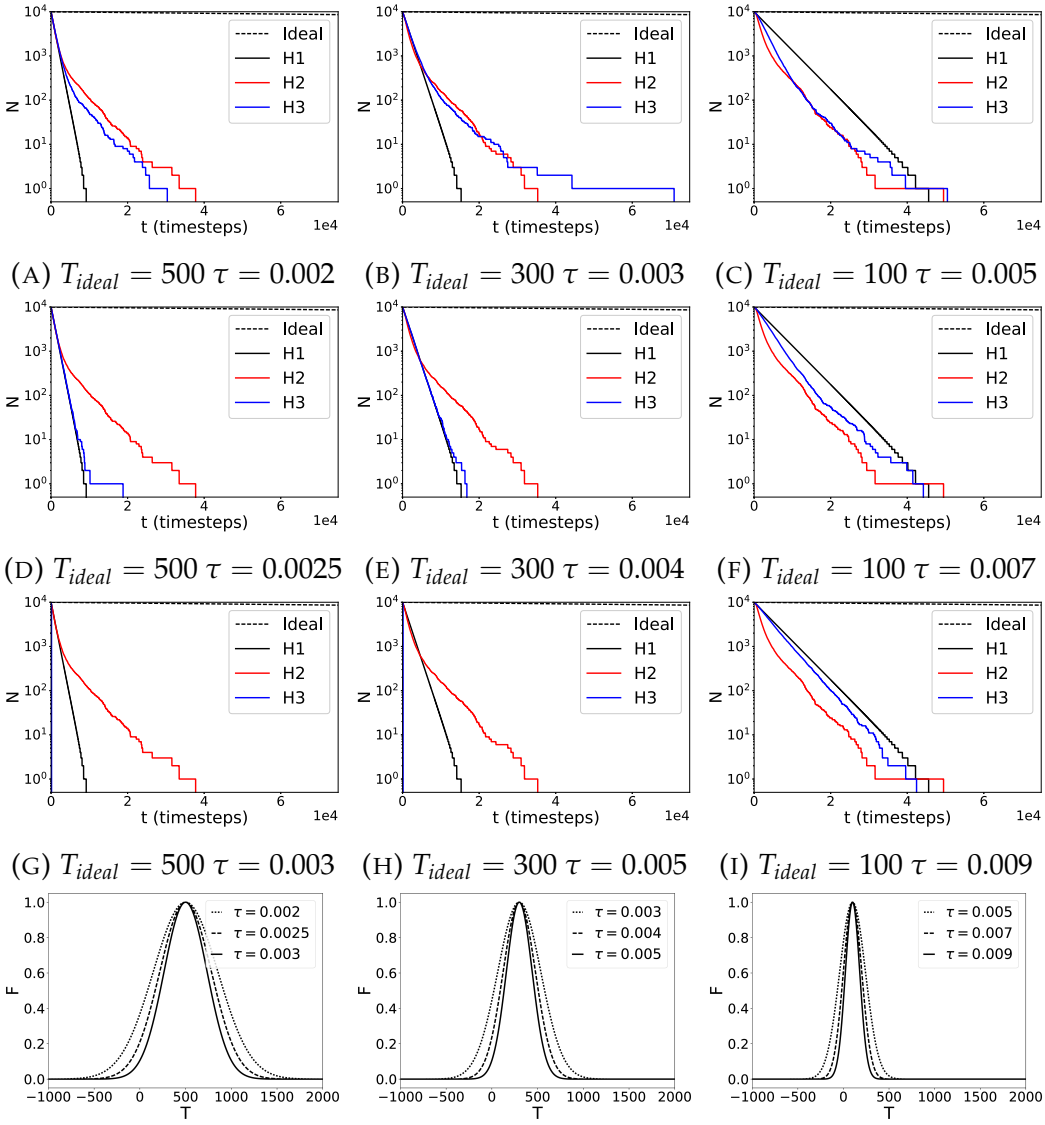
(A) System 1 (B) System 2 (C) System 3

(D) System 1 (E) System 2 (F) System 3

FIGURE 5.4: Temperature vs time and total population vs time for individual H3 systems with $T_{ideal} = 300$ and $\tau = 0.003$. In the temperature figures T_0 is shown as a black horizontal line, and T_{ideal} is shown in green.

We ran similar survival experiments to those shown in Figure 5.3 with H3 systems (see Figure 5.5). Whether the added feedback from the environment to the microbes helps or hinders an H3 biosphere's survival probability depends on how far the starting conditions are from T_{ideal}, and the value of τ. H2 biospheres can be though of as a limiting case of H3 biospheres with microbe sensitivity $\tau = 0$. Figure 5.5 shows the results of experiments with varying T_{ideal}, and τ values for H1, H2, H3 and 'Ideal' systems.

The first column in Figure 5.5 shows systems where $T_{ideal} = 500$ and τ (microbe sensitivity) increases for H3 biospheres as we move down the column. Figure 5.5a, with $\tau = 0.002$ shows feedback hindering the H3 biospheres' survival rates compared to H2 systems where $T_{ideal} = 500$. As τ



(A) $T_{ideal} = 500$ $\tau = 0.002$ (B) $T_{ideal} = 300$ $\tau = 0.003$ (C) $T_{ideal} = 100$ $\tau = 0.005$

(D) $T_{ideal} = 500$ $\tau = 0.0025$ (E) $T_{ideal} = 300$ $\tau = 0.004$ (F) $T_{ideal} = 100$ $\tau = 0.007$

(G) $T_{ideal} = 500$ $\tau = 0.003$ (H) $T_{ideal} = 300$ $\tau = 0.005$ (I) $T_{ideal} = 100$ $\tau = 0.009$

(J) Fitness vs T for $T_{ideal} = 500$ (K) Fitness vs T for $T_{ideal} = 300$ (L) Fitness vs T for $T_{ideal} = 100$

FIGURE 5.5: Number of surviving biospheres (N) against time, for experiments with differing T_{ideal} and τ (microbe sensitivity) values. For all experiments $T_0 = 0$.

increases slightly to $\tau = 0.0025$ (Figure 5.5d), the H3 biosphere survival rates are reduced more. Figure 5.5g, where $\tau = 0.003$, shows that with strong enough feedback H3 systems rapidly go extinct and highlights a feature of H3 systems that is not present in H2 systems – extinction via starvation. As H3 microbes are temperature sensitive, if they find their environment too inhospitable they will be unable to consume nutrients and the biosphere will quickly go extinct. In Figure 5.5g, microbes are seeded in an environment they cannot tolerate, dooming them to a rapid extinction. Figure 5.5j shows the fitness curves for the H3 microbes against temperature for each of the τ

values explored when $T_{ideal} = 500$.

Figure 5.5's second column shows experiments with $T_{ideal} = 300$. Figure 5.5b show experiments with $\tau = 0.003$ for H3 microbes. Comparing Figures 5.5g and 5.5b shows how the survival rates of biospheres with the same τ value can differ with different T_{ideal} values. Moving T_{ideal} closer to T_0 in Figure 5.5b not only prevents immediate starvation of H3 microbes, as seen in Figure 5.5g, but allows a few H3 systems to out live all H2 systems. With stronger feedback, 'anti-Gaian' dynamics can be more strongly countered provided the early biosphere is able to survive. Figure 5.5e shows that increasing τ, this time in larger increments, again starts to hinder the survival rates of H3 systems as the early biospheres struggle to establish themselves and / or become 'stuck' in the temperature limiting regimes. Figure 5.5h with $\tau = 0.005$ shows the H3 systems rapidly going extinct via starvation as the microbes are unable to survive their initial environment. Figure 5.5k shows the H3 microbes' fitness curves for the τ values explored for $T_{ideal} = 300$. The widest fitness curve in Figure 5.5k corresponds to the narrowest fitness curve in Figure 5.5j but shifted to the left as T_{ideal} moves closer to $T_0 = 0$.

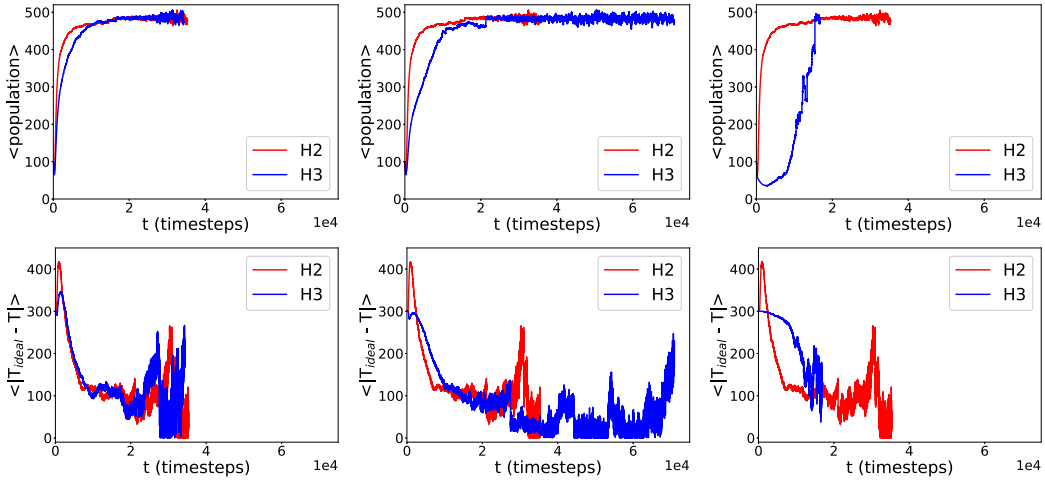
The third column in Figure 5.5 shows biospheres with $T_{ideal} = 100$. Here we see that H3 systems overall experience higher survival rates over H2 systems for the range of τ explored. Comparing Figures 5.5h and 5.5c we see that keeping $\tau = 0.005$ constant, but moving T_{ideal} closer to T_0, the survival rates of H3 systems are vastly improved, again demonstrating that the positive or negative impact environmental feedback can have on biospheres' survival rates is strongly dependant on the starting environmental conditions. As we increase τ to $\tau = 0.007$ (Figure 5.5f) and $\tau = 0.009$ (Figure 5.5i) we see that, in the survival rate for H3 systems is increasing – feedback improves H3 biospheres prospects for long term survival. Figure 5.5l shows the fitness curves for the H3 biospheres in column 3, and shows that such strong feedback, not possible in previous experiments where T_{ideal} was further from T_0, is both possible and beneficial when initial conditions are close to the microbes ideal environment.

When $T_{ideal} = 100$, the H3 systems in general have poorer survival rates than H1 systems despite performing better than H2 systems. With strong environmental feedback the H3 biospheres are more likely to be temperature limited than nutrient limited as the window of temperatures allowing for nutrient limitation shrinks as τ increases, meaning that the temperature is more likely to perform a random walk to either T^+_{lim} or T^-_{lim} and become 'stuck' there. This prevents the temperature from diverging far from T_0 as

happens in the unconstrained H2 systems, however it also prevents temperatures from reaching values closer to T_{ideal}. As $T^{-}_{lim} < T_0$ must be true for a viable biosphere, the P_T values of H3 systems in a temperature limited regime are greater than $P_{T,0}$ and so in general H3 biospheres experience poorer survival rates than H1 biospheres when T_{ideal} is close to T_0 even with strong feedback.

4 .3 Comparing H2 and H3 systems

We compared how the average populations and temperatures of H2 and H3 systems behaved over time in extant systems. Figure 5.6 shows the average population and average $|T_{ideal} - T|$ over time, for those biospheres still alive at each timestep. $T_{ideal} = 300$ in each case and $\tau \in \{0.002, 0.003, 0.004\}$. These τ values differ slightly to those used in Figure 5.5 to show the impact of weak feedback, where H2 and H3 systems can behave very similarly, and because $\tau = 0.005$ for $T_{ideal} = 300$ results in biospheres going extinct too rapidly for interesting analysis.



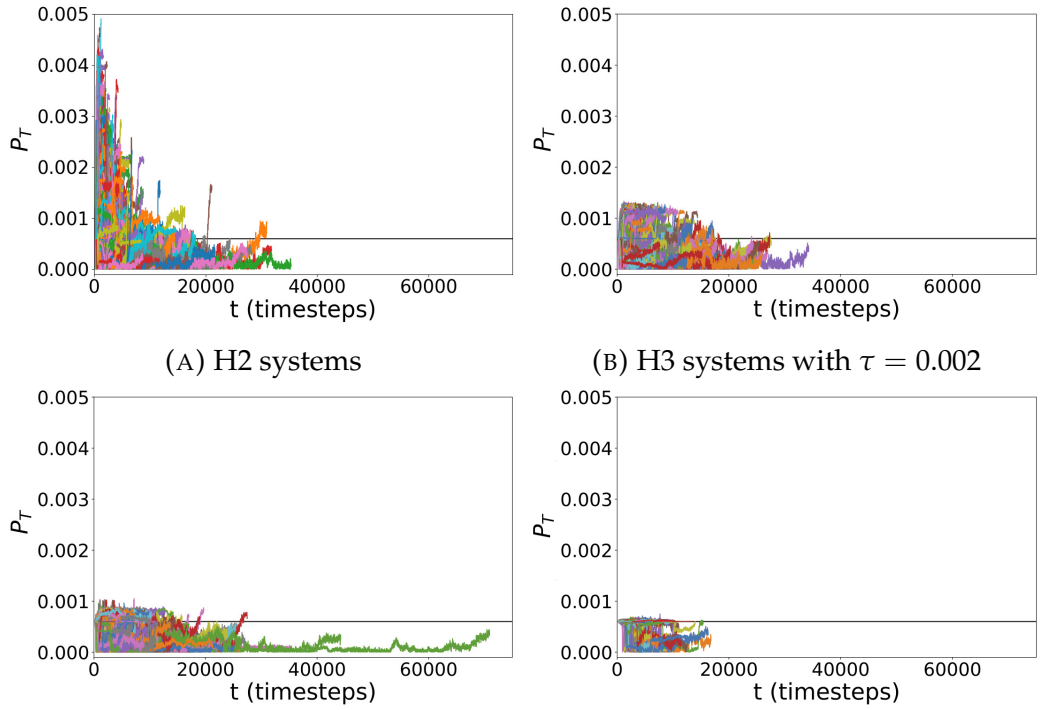
(A) $T_{ideal} = 300$ $\tau = 0.002$ (B) $T_{ideal} = 300$ $\tau = 0.003$ (C) $T_{ideal} = 300$ $\tau = 0.004$

FIGURE 5.6: Averaged population, and averaged $|T_{ideal} - T|$ of surviving H2 and H3 systems over time.

The top panel in Figure 5.6 shows that the population in H3 biospheres on average grows more slowly than in H2 biospheres. With feedback, as $T_0 \neq T_{ideal}$, the growth rate of H3 microbes is initially slow compared to the temperature insensitive H2 microbes. The stronger the feedback on microbe metabolisms, the longer it will take for H3 biospheres to reach the environmental carrying capacity. With strong enough feedback H3 biospheres can

remain in a temperature limited regime, instead of a resource limited regime – the case for all H2 biospheres.

With a lower reproduction rate, mutants are slower to appear in H3 biospheres, causing early temperature changes in the system to be slower than for H2 biospheres. The lower panels in Figure 5.6 show the average $|T_{ideal} - T|$ values for H3 and H2 extant systems over time. The H2 systems (in red) show an initial increase in this value, showing that many systems are degrading their environment. These systems will be short lived as they will have higher P_T values, and quickly the average $|T_{ideal} - T|$ value drops, as those H2 biospheres that improve their environment survive via selection by survival. The H3 systems (in blue) do not show such a marked initial increase in $|T_{ideal} - T|$. With feedback, degrading H3 biospheres are self limiting. The early fitness of H3 biospheres is also lower than for the temperature insensitive H2 biospheres, and so H3 systems can get 'stuck' close to T_0 as new mutants take longer to appear.



(A) H2 systems

(B) H3 systems with $\tau = 0.002$

(C) H3 systems with $\tau = 0.003$

(D) H3 systems with $\tau = 0.004$

FIGURE 5.7: Figures showing the P_T values for H2 and H3 systems values for all experiments, with $T_{ideal} = 300$. The P_C constant extinction probability is shown in black in each figure.

Figure 5.7 shows the P_T extinction values for $T_{ideal} = 300$, with $\tau \in \{0.002, 0.003, 0.004\}$ for the H3 experiments. The constant null P_C extinction probability is shown in black in each figure. Figure 5.7a shows the H2 experiments,

and we see that early on, many H2 biospheres perturb their environment in a way that greatly increases their P_T extinction probability (initially all have the value indicated by the black horizontal P_C line). These systems however are short lived, and we see that over time, only those biospheres with smaller and smaller P_T survive. Figures 5.7b - 5.7d show H3 biospheres with increasing τ. We see that with feedback to the microbes, the biospheres are unable to reach the high extinction probabilities reached in the H2 biospheres. As the microbes sensitivity increases, the H3 biospheres become less able to increase their P_T values over the starting P_C value, as doing so prevents their ability to consume nutrients resulting in starvation if conditions do not improve – thus 'anti-Gaian' dynamics are strongly self limiting when τ is high. This same feedback can hinder a H3 biosphere's ability to reach very low P_T values and thus can also hinder long term survival rates (Figure 5.7d).

5 Discussion

Demonstrating the efficacy of selection-by-survival is potentially important for understanding how ecosystems or biogeochemical cycles may 'evolve' (Bouchard, 2014; Bourrat, 2014). Our models suggest that selection by survival alone – the chance acquisition of beneficial adaptations – can promote long-term persistence of simple biospheres.

'Selection by survival' has been presented as a way to reconcile natural selection and the Gaia hypothesis without invoking selection *for* global homeostasis on the level of the biosphere. However, the absence of feedbacks between life and the abiotic environment means that in its simplest form it falls short of what is usually considered 'Gaia'. Our work shows that biospheres that incorporate environmental feedbacks on growth can additionally prevent 'anti-Gaian' dynamics from occurring and thereby further enhance their persistence. This situation supports the central idea of the Gaia hypothesis – namely that regulation can emerge from the interaction of life and the abiotic environment.

The role of feedbacks is strongly dependant on the early conditions of the system. Feedbacks can prevent young biospheres from expanding as rapidly as in their absence, but over longer time-spans surviving biospheres that include feedbacks can have significantly lower extinction probabilities than those without, depending on starting conditions. This means that early life attempting to become established on an inhospitable planet could be held

back by environmental constraints, but in environments closer to ideal habitable conditions, feedbacks help to maintain that habitability. This result corresponds to the idea of 'Gaian-bottlenecks' (Chopra and Lineweaver, 2016) where early in a planet's history, the biosphere must quickly establish self-regulatory feedback mechanisms, or face extinction.

For 'randomly walking' systems, such as the models presented, the probability of reaching a point far from the starting position increases with the number of 'steps' taken – in our model, the number of mutations occurring in the biosphere. Our model systems start far from ideal conditions, and those whose random walk do not improve conditions have a high risk of extinction. Taken together, these points illustrate the importance of a guided random walk mechanism for the very long-term persistence of life on a planet.

Feedback between life and the environment is an inevitable feature of any biosphere, including the Earth. Furthermore, once a planet has abundant life it will inevitably become a significant driver of global biogeochemical cycles. We argue that both selection by survival and environmental feedback are likely to be important explanatory factors in any long-term persistence of life. The outstanding empirical challenge is to identify these two mechanisms amidst the complexity of Earth's biosphere and to resolve their relative contributions to the persistence of life on Earth – i.e. to determine whether Gaian regulation is a weak or strong stabilising force.

A Alternative Mechanisms for Gaia – Appendix

A .1 Model Description

The code used to generate the data for H2 and H3 systems is heavily based on a previous model called the Flask model (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010; Nicholson et al., 2017).

The Flask Environment

We have a single well mixed environment with no spatial element – we assume that in the flask the liquid medium is well mixed so that the composition of the flask is in a homogeneous steady state. The flask is characterised by nutrient levels and temperature. The nutrients present may be consumed by microbes and converted into biomass. The temperature is affected by and can affect, for H3 systems, the microbe activity.

The state of the flask is given by a vector V:

$$V = (n_1, ..., n_N, T) \tag{5.4}$$

where n_i is the concentration of nutrient i, N is the number of nutrients, and T is the flask temperature.

As we break down each timestep into a number of iterations n where n is the total population of the system at the start of the timestep, we break down the inflow and outflow of the nutrient flask medium to prevent sudden changes at the the start of each timestep. The steps within a timestep would ideally all be computed in parallel but computational limitations prevent this, and so for agent based dynamics we effectively freeze the system while the selected microbes performs an action (being nutrient consumption / biomass production / reproduction / death). If we simply added and deducted the flow amounts at the start of each timestep, microbes selected at the beginning of a timestep could see a very different world to those selected at the end of a timestep if the population is large due to the microbes effect on the environment (nutrient consumption reducing nutrient levels and biomass creation affecting the abiotic parameters). Although these effects would largely average out due to the random selection of microbes during each timestep, a single large influx per timestep could be thought of as a periodic perturbation on the system which could affect the results seen. To

counter this, we calculate the net influx of nutrients N_{net} at the start of each timestep:

$$N_{net} = I_N - O_N \times N_{current} \tag{5.5}$$

where I_N is the number of units of nutrient inflow per timestep, O_N is the percentage outflow, and $N_{current}$ is the current nutrient levels in the system at the start of the timestep. We can then do $N_{step} = N_{net}/K_{current}$ where $K_{current}$ is the total population of the system at the start of the timestep, and then for each iteration within a timestep we increment the nutrient levels by N_{step}. This results in the same quantity of nutrients being added / removed from the system as if there was just one update at the start of the timestep, but it results in a much smoother transition and means that microbes selected at the start and end of a timestep will see much more similar worlds. In doing this, we treat nutrient levels as continuous but the microbes can only ever treat the nutrients as units. So while each iteration we might be adding 10.7 nutrient units per iteration, any microbes in the system can only act on the integer amounts of nutrients present.

We calculate the net temperature change due to diluting the current flask medium, by removing certain percentage I_T of the existing flask medium and replacing it with the same volume of fresh influx at temperature T_{inflow}. So for the flask temperature we update each iteration by T_{net}:

$$T_{net} = T_{inflow} \times I_T - T \times I_T \tag{5.6}$$

again each timestep we can then increment the flask temperature by $T_{step} = T_{net}/K_{current}$ where again $K_{current}$ is the total population of the system at the start of the timestep.

Microbes

The microbes consume and excrete nutrients in fixed proportions and affect the temperature of their environment as a side effect of biomass creation. The ratios of nutrient consumption / excretion and the byproduct effect on the temperature are genetically encoded for each microbe species. All microbes share the same preferred temperature T_{ideal} (i.e. the temperature which results in the maximum growth rate). Microbes grow by consuming nutrients and converting them to biomass, and they reproduce asexually by splitting once their biomass reaches a threshold. Biomass is reduced by a fixed amount per timestep to represent the cost of staying alive. Microbes die if

their biomass drops to a fixed threshold, which can happen during nutrient limitation or temperature limitation causing the microbes being unable to consume the nutrients present.

In the code we do not record microbes of the same species individually as doing so would slow the code considerably. Instead we group microbes of the same species together and record the species' total biomass. Thus each species can be thought of as a vector S:

$$S = (G, K_S, B, F, W, T_{ideal}) \tag{5.7}$$

where G is the species' genome (represented as a decimal number), K_S is the population of the species, B is the total biomass of the species, F is total number of consumed food particles not yet converted into biomass, W is the total number of waste particles not yet excreted by members of the species, and T_{ideal} represents the temperature that maximise the growth for microbes in species S.

The genotype G of a microbe is recorded as the decimal representation of an 8 bit binary string, and this is used to group microbes into species. Microbes that share the same genome are of the same species. We create tables for microbe nutrient / excretion rules and abiotic effects and this genome is used as the reference to look up the particular metabolism rules for a microbe. With an 8 bit long binary genome there are 256 possible species (as each 'gene' in a genome can have the value 0 or 1).

Microbes consume and excrete nutrients following genetically determined ratios. The nutrient ratios are fixed at the start of each simulation for each genome and remain constant. For example, with 4 nutrients: a, b, c, d, a microbe might need to consume nutrients with a ratio $\frac{1}{3}$ nutrient a and $\frac{2}{3}$ nutrient b, and excrete a ratio of $\frac{1}{2}$ nutrient c, and $\frac{1}{2}$ nutrient d. This would be recorded in a vector as $[\frac{1}{3}, \frac{2}{3}, -\frac{1}{2}, -\frac{1}{2}]$. Positive values indicate that that nutrient is consumed, and negative that it is excreted by the microbe. We generate the look up tables for microbe metabolisms in the following way:

To generate these vectors for each genome, we start with 2 vectors of length N where N is the number of nutrients. We populate these vectors with random numbers generated between $[-1, 1]$ and then sum. For example if we had 4 nutrients, and our two vectors were $[-0.3, 0.1, 0.5, 0.6]$ and $[-0.2, -0.2, 0.1, -0.9]$ then summed we would have: $[-0.5, -0.1, 0.6, -0.3]$. This would lead to the following ratios for consumption / excretion: $[-\frac{5}{9}, -\frac{1}{9}, 1, -\frac{3}{9}]$. A microbe with this metabolism would only eat nutrient c and would excrete nutrients a, b, and d. Not all metabolisms generated in this way will

TABLE 5.1: Example microbe metabolism look up table with 4 nutrients a, b, c, and d

G	a	b	c	d
0	1/2	-1/3	-2/3	1/2
1	1/8	3/8	1/2	-1
2	-1/5	-3/5	1	-1/5

be viable. For example if the maximum possible number of nutrients a microbe can consume is $C^{max} = 10$ then the following metabolism $[\frac{5}{12}, \frac{7}{12}, -\frac{1}{8}, -\frac{7}{8}]$ would be unviable. This metabolism would require a microbe to consume 5 units of nutrient a at the same time as 7 units of nutrient b, however this is never possible if $C^{max} = 10$. Units of nutrients are non divisible and can only be consumed in integer amounts. Thus any microbes with this metabolism would quickly starve to death. Generated metabolism vectors that result in all positive or all negative values are discarded, as microbes must both eat and excrete, and a new vector is generated for that genome. Table 7.4 shows an example look up table. To use Table 7.4, for a microbe with genome 000000010, we convert to its decimal value, 2, and find that this microbe has metabolism where it consumes only nutrient c, and returns waste nutrients with the ratio $\frac{1}{5}a$, $\frac{3}{5}b$ and $\frac{1}{5}d$.

Metabolism The microbes convert their food into biomass in an inefficient process that produces waste product. The efficiency of this conversion is given by θ, and the amount of biomass produced is given by:

$$B_j = \theta F_j \tag{5.8}$$

where B_j is the number of biomass units produced and F_j is the number of food units currently 'contained' with a microbe j. The waste excreted in this process is given by:

$$W_j = (1 - \theta) F_j \tag{5.9}$$

where W_j is the number of waste units produced, which are released into the environment after the biomass has been created, in the form determined by the microbe j's specific metabolism.

Effect of temperature on metabolic rate The system temperature affects the rate at which microbes can consume nutrients which in turn affects the rate of biomass production and thus the growth of the microbes. A microbe

will attempt to consume a maximum amount C_j of nutrients each timestep with the demand being met depending on nutrient availability. The C_j is calculated for each microbe j as a function of the match between the microbes' genetically specified T_{ideal} and the current temperature of the flask environment. This function has a Gaussian form and falls away smoothly from its maximum as the distance between the optimum and the current environment increases. Mathematically we write this as:

$$C_j = \psi_j C^{max} \tag{5.10}$$

$$\psi_j = e^{-(\tau|T_{ideal}-T|)^2} \tag{5.11}$$

where C^{max} is a constant determining the maximum possible rate of consumption for any microbe, ψ_j is a microbe specific measure of the microbe's satisfaction with the current abiotic environment, τ is a universal constant parameter that determines how sensitive the microbes are to their environment ($\tau = 0$ means the microbes are not affected by the abiotic environment at all, and a higher τ means the microbes become more sensitive to the abiotic conditions). p_j is a measure of the distance between the current temperature T, and the microbes preferred temperature T_{ideal}.

$\tau = 0$ turns off any feedback from the environment to the microbes. This τ value is the only parameter that was changed between H2 and H3 systems. For all H2 systems $\tau = 0$, for H3 systems $\tau > 0$.

Effect of microbial activity on environment Microbes can affect the system temperature as a side effect of biomass creation. The effect the microbe has is proportional to its rate of biomass creation and thus its growth rate, so faster growing species will have a larger effect than slower growing species. Through the consumption of nutrients and excretion of waste products microbes also affect the nutrient levels in the environment.

Each microbe has an effect on the system temperature per unit of biomass created, and these effects are numbers in the range $[-1, 1]$. These numbers are randomly generated in this range at the beginning of each simulation for each species and remains constant throughout the simulation. Thus each member of a species has the same effect on the system temperature for the duration of the simulation.

Maintenance Cost There is a fixed biomass cost λ of staying alive for each microbe. This reduces a microbe's biomass by a constant rate. This cost represents the energy costs of maintaining cellular machinery and metabolic inefficiency. This cost is assumed to be lost as unrecoverable heat radiation. This ensures that the chemicals cannot be infinitely recycled and it sets the carrying capacity of the system. This carry capacity is reached when the total heat dissipation matches the energy supplied in the form of chemicals, i.e. the food the microbes consume. λ is identical for all species.

Reproduction and Mutation If the microbe is able to consume enough chemicals to reach the reproduction threshold T_R, it will reproduce asexually, splitting in half. Half of the biomass with go to the new microbe and the parent microbe will be left with half its biomass. The new microbe will have the same genome as the parent unless a mutation occurred during the reproduction. There is a small constant probability of mutation, P_{mut}, for each locus. During a reproduction event, the code iterates through the genome of the new microbe and if a mutation occurs at a locus then the gene at that point will be 'flipped', turning it to 0 if it were previously 1, or to 1 if it were previously 0. This new mutant genome will then dictate the new microbe's metabolism.

Death If a microbe's biomass falls to a starvation threshold B_D the microbe will starve to death. There is another small probability of death D that represents death by hazardous mutation or damaging local environmental changes etc. When a microbe dies its biomass is removed from the system, as if the dead microbe, for example, fell to the bottom of the ocean. During a death event, we first check to see if the selected microbe has enough biomass to avoid death by starvation. If the microbe has not starved to death it will be killed with probability D.

Selecting a microbe

We use agent based dynamics in our model. This means within a timestep, a microbe is chosen randomly for an event and time is effectively frozen while the microbe performs that event. Time is then restarted and another microbe is chosen at random for an event.

As we record microbes grouped together in a species (Equation 5.7), for any particular species we have the population of the species, the total species

biomass, and the total consumed food not yet converted into biomass. To select a single individual of a particular species we therefore need to determine how much biomass and unconverted food this individual has. If a microbe is selected for a reproduction event, we need to know how much biomass it has to know if it has reached the reproduction threshold for example.

There will be variation between individuals of a species and so we assume a normal distribution of biomass and unconverted food between individuals of a species. The biomass normal distribution is centred around the average amount of biomass B_{av} per microbe (i.e. the total species biomass divided by the species population), with standard deviation of the distribution is $B_{av} \times 0.1$. The normal distribution for the unconverted food is the same but with F_{av}, the average amount of unconverted food per microbe, instead. The standard deviation for both distributions is small, resulting in a small level of variation in the population. Therefore most individuals of the same species will have the same biomass and food levels.

Once we have selected a microbe and calculated its biomass and food level, the microbe can then attempt to perform the event it was selected for.

A .2 Biosphere-wide extinction probabilities

The probabilities of biosphere-wide extinction are determined in the following way:

H1 systems

For the null model we assume a constant extinction probability for each biosphere at each model timestep, resulting in exponential decay in the number of surviving biospheres. The probability of extinction for all time for H1 systems is a constant:

$$P_C = C \tag{5.12}$$

We set C to have the same value as the starting extinction values for the selection by survival, and the added feedback experiments.

H2 and H3 systems

For our H2 and H3 systems, the flask temperature impacts the biosphere-wide probability of extinction:

$$P_T = a + b \times |T_{ideal} - T| \tag{5.13}$$

T is the system temperature, and depends on the genetic makeup of the microbe community currently alive in the system, $a = 2 \times 10^{-6}$ is a constant background probability of global extinction, and $b = 2 \times 10^{-6}$ controls the impact the flask temperature has on the probability of extinction. Here T_{ideal} – the temperature for which microbes have the highest fitness is also the flask temperature that results in the lowest probability of flask extinction.

A .3 Parameters

The parameters used for the flask systems presented in the paper are found in Table 5.2.

A .4 Method

H1 systems

For the null model we simply apply the biosphere-wide extinction probability P_C to 10^4 H1 systems until all are extinct. This is an exponential decay.

H2 and H3 systems

We again run 10^4 experiments for each scenario. In each experiment we seed the flask with a single species, and we fix this species to have $\alpha = 0$ impact on the flask temperature per biomass created. This means all flask systems start with identical starting conditions, and any differences in flask experiments is due to the mutants arising in the system, and not due to differing starting configurations.

We use agent based dynamics to run the H2 and H3 simulations. A timestep is broken down into iterations, the number of iterations matches n the number of microbes alive in the system at the start of the timestep. For each iteration we perform the following steps:

- We run the inflow and outflow of the nutrient rich flask medium for 10^4 timsteps to reach an equilibrium state before seeding
- Seed with 100 microbes of the same species with $\alpha = 0$ impact on the flask temperature per biomass created
- For each iteration we perform the following steps:

TABLE 5.2: Model parameters

N	4	Number of nutrients
B_R	120	Reproduction threshold (biomass units)
B_D	50	Starvation threshold (biomass units)
P_{mut}	0.01	Probability of mutation at each locus during reproduction
D	0.002	Probability of death by natural causes (other than starvation) at each timestep
λ	1	Maintenance cost (biomass units / timestep)
θ	0.6	Nutrient conversion efficiency
C^{max}	10	Maximum number of nutrients a microbe can consume in any single event
τ	[0.002, 0.0025, 0.003, 0.004, 0.005, 0.007, 0.009]	Level of influence of abiotic environment on metabolism
μ	[-1,1]	The impact a microbe has on the flask temperature per biomass created is taken from this range.
I_N	150	Rate of nutrient influx (units / timestep)
O_N	0.25	Rate of nutrient outflux (percentage / timestep)
I_T	0.2	Percentage of flask medium replaced with fresh influx each timestep, used for calculating the flask temperature change (percentage / timestep)
K_M	100	Number of individuals in flask inoculum
t_{prep}	500	Flask equilibration time prior to seeding (timesteps)
T_{ideal}	[500, 300, 100]	The temperature at which the biosphere-wide extinction probabilities are at a minimum, and the universal microbe temperature preference
T_{inflow}	0	Environmental temperature in the absence of microbe activity

  - Influx / outflux of flask medium (at constant temperature) and nutrients via trickle
  - An individual is selected randomly for a death event
  - An individual is selected randomly for a nutrient consumption event
  - An individual is selected randomly for a biomass creation event
  - An individual is selected randomly for a reproduction event

- We repeat this process n times for one timestep.
- Each timestep, the flask system has the temperature dependant probability P_T of going extinct.
- Each simulation is run until the system goes extinct.

Chapter Summary

In this Chapter I have explored an adaptation of the single-flask model (Chapter 4) to explore the hypothesis of selection by survival (Doolittle, 2014). In the model described, flask systems now have a global probability of total extinction that depends on the global temperature. A null model was explored where systems simply have a constant rate of total extinction and then this null was compared to two cases – pure selection by survival where microbes impact their global temperature as in the typical single-flask model, but they themselves are not impacted metabolically by the global temperature. In this scenario microbes may improve their habitability prospects by pushing their environmental temperature towards the temperature which minimises the chances of global extinction via a 'random walk' where there system moves the temperature as determined by the composition of the microbe community at any point in time. However there is no mechanism baring 'luck' whereby a system can maintain a 'safer' temperature as microbes themselves individually are insensitive to it, and thus no feedback is possible.

The null hypothesis and this pure selection by survival case were then compared to a scenario where microbes are now temperature sensitive and suffer if the temperature deviates too far from their 'ideal' temperature where their metabolism is at a maximum. The results found that selection by survival with feedback can result in greater survival prospects for systems, however now the starting conditions of the flask environments are far more important, as if the initial temperature is too far from ideal conditions life will rapidly go extinct. However with feedback, once life is established in the system 'anti-Gaia' dynamics, where life pushes its environment far from habitability and thus causes its own extinction, are avoided and thus systems with feedback can have increased persistence probabilities.

The null case, and the case where selection by survival is explored without feedback are less realistic scenarios than the final case including feedback. As all life impacts its environment and is itself impacted by its environment feedback loops are inevitable for any biosphere. Therefore both feedback and selection by survival will play a role in explaining the Earth's long history of inhabitance. Both of these will also inform our search for exoplanets and alien life, which takes us to the next part of my thesis where I look beyond Earth's horizons, and consider what the Gaia hypothesis can tell us about alien worlds.

Chapter 6

Habitable Exoplanets and Alien Life

In this thesis so far I have explored the Gaia Hypothesis while focusing on the Earth and how a Gaian way of thinking can help explain the long continued habitability of the Earth. However clearly the Gaia hypothesis applies to any planet hosting life (indeed it was contemplating life on Mars which first inspired the hypothesis). In this Section, I will expand my discussion beyond the Earth's horizons and provide a brief overview on the field of Astrobiology, and where our search for alien life, and potentially habitable Exoplanets, currently stands.

We only know of one planet with life, one planet with complex interactions between the abiotic planet and the biosphere, and so naturally much of the Gaia debate has centred around Earth and understanding Earth's long term continued habitability. However, humans have long contemplated the night sky and the objects moving above us. When humans realised that the Earth is not alone, and that other rocky planets exist next door, these planets captured our collective imagination, and the possible existence of alien life has been a major drive in some areas of scientific research. Not only is this question – "are we alone?" – interesting scientifically, it also touches something deep within the human mind. We are a social species, susceptible to loneliness, and a species intelligent enough to contemplate the stars, even to visit worlds beyond our own. Whether or not there is life beyond our planet, perhaps even intelligent life, will deeply affect how we view ourselves and our place in the universe.

1 Alien life in our Solar System?

As rocky planets, close to Earth, and easy to see on a clear night, both Venus and Mars have been the subject of speculation as hosts of alien life, both

past and present. Although having vastly different surface conditions today (Figure 6.1) Mars a dry frozen planet, Earth wet and teeming with life, and Venus a dry planet with surface temperatures over $700K$, all three planets are thought to once have looked far more similar. Early in the history of our Solar System, all three planets are thought to have had abundant water and habitable surface conditions (Donahue et al., 1982; Pollack et al., 1987; Squyres and Kasting, 1994; Way et al., 2016). Did our solar system once host Martian or Venusian life? If so could any of this life have survived to today? Where the present states of Mars, Earth, and Venus inevitable, or is it possible that the Earth 'got lucky' in retaining its habitability while Venus and Mars had similar prospects but lost the dice roll.

(A) Venus (B) Earth (C) Mars

FIGURE 6.1: The Earth with its nearest neighbours, Venus and Mars. These planets although near one another are vastly different on the surface. Image credit: NASA

1 .1 Venus

As the second brightest (natural) object in the night sky, Venus, named after the Roman goddess of love and beauty, has inspired human culture for thousands of years. Civilisations as far back as the ancient Sumerians have recognised it as a single celestial object (Cooley, 2008) and it was the first planet to have its motions across the sky recorded as early as 2000BC (Evans, 1998). In more recent times, Venus, as the closest planet to the Earth, orbiting the Sun at 0.72 AU, was a prime candidate for planetary exploration. Due to the high albedo of Venus, caused by its dense cloud cover, surface conditions on the planet remained a mystery until humans sent spacecrafts to the planet to investigate. It was portrayed as having a warm climate, water rich, and possibly teaming with life in popular fiction in the early to mid 20th century (Miller, 2003), for example H. P. Lovecraft and Kenneth Sterling's "In

the Walls of Eryx", published in 1939, which takes place on a Venus covered in muddy Jungle, inhabited by humanoid lizard creatures.

In 1962 the Marina 2 (*Marina 2 mission* 1962) spacecraft became the first human made object to visit another planet when it arrived at Venus. It revealed that Venus has cool clouds, and an incredibly hot surface. In 1970, the Venera 7 (*Venera 7 mission* 1970) successfully landed on the surface of Venus, and transmitted data that informed us that Venus's thick atmosphere is composed 97% of CO_2 and that the planet has a surface temperature of $475 \pm 20^o C$ and a surface pressure of 90 ± 15 Earth atmospheres. Similar pressures on Earth are found roughly 900m below sea level. Venera 7 provided definitive proof that life as we know it could not survive on Venus and confirmed that surface water could not exist on the planet. The first photographs of the surface of Venus were taken by the Venera 9 spacecraft. Figure 6.2 shows an image of the surface of Venus, taken by the most recent lander to visit Venus -the Venera 14 which landed in 1982. The high surface temperatures and pressures make it difficult for machinery to survive long on Venus and the highly hostile surface conditions leave little hope for finding Venusian life.

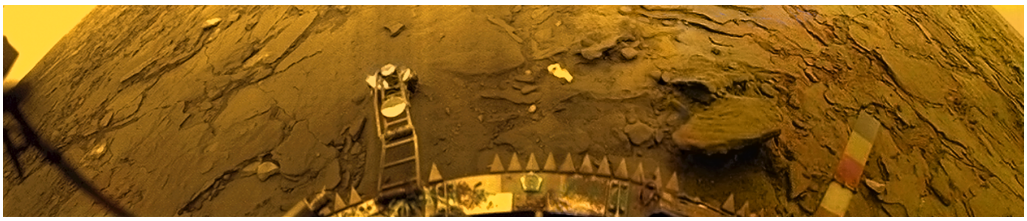


FIGURE 6.2: Photo taken by the Venera 14 lander of the surface of Venus. Credit: Russian Academy of Sciences, processing by Ted Stryk

Although Earth and Venus's surface environments are vastly different today – one teeming with life, the other far too hot for liquid water – the composition of both, their size and their mass, are very similar. Because of this Venus is sometimes referred to as Earth's sister planet. (Lopes and Gregg, 2004). Due to the different surface conditions today, Venus and Earth are traditionally thought to be different classes of planet, despite their numerous similarities. Venus's closer orbit to the Sun is thought to have doomed it to its current state. Evidence suggests that Venus once hosted large bodies of water (Donahue et al., 1982; Jones and Pickering, 2003; Svedhem et al., 2007), which since boiled away due to a runaway greenhouse effect (Kasting, 1988) leading to Venus's present surface temperature of over 400^oC. This runaway greenhouse event is traditionally thought to have been inevitable due to Venus's close orbit around the Sun.

Although finding life resembling that found on Earth on Venus today would be highly improbable, possible present day refuges for life on Venus have been suggested such as the upper atmosphere where temperatures are far lower, or in high pressure subsurface water habitats (Schulze-Makuch and Irwin, 2002).

1 .2 Mars

Mars has also been long known to humanity and associated with various gods. It was known as 'The Red One' to ancient Egyptians, Nergal the star of death to Babylonians, and Ares to ancient Greeks (Sheehan, 1996). Mars orbits at 1.67AU from the Sun and in many ways is the opposite extreme to Venus. It has an incredibly thin atmosphere less than 1% of Earth's with a mean pressure of just 0.6% of Earth's, leaving little protection from the Sun's radiation, nor helping the planet to retain heat. Surface temperatures on Mars vary around a mean value of -55^{o}C. Surface temperatures may reach 20^{o}C at Martian 'noon time' at the equator and temperatures at the poles may drop to temperatures of -153^o. It is roughly half the diameter of Earth, has 15% of the Earth's volume and 11% of the Earth's mass. A Martian magnetosphere once existed however this was lost 4 billion years ago, perhaps due to numerous asteroid impacts (Hood et al., 2003). Without a magnetosphere, the solar wind interacts directly with the Martian ionosphere causing the density of the atmosphere to drop by stripping away atoms.

Mars has been considered as a host for alien life for hundreds of years. In 1877, Italian astronomer Giovanni Schiaparelli produced the first map of Mars as telescope technology had advanced such that surface features could be identified (Schiaparelli, 1882). These maps of Mars contained 'canali' – long straight features on the surface of Mars, later shown to be an optical illusion (Yeffeth and Wells, 2005). This Italian word for 'channels' or 'grooves' was mistranslated into English to be 'canals'. American astronomer Percival Lawrence Lowell was one of the strongest proponents of the idea of canals having been built by an intelligent race of Martians to fight against the decline of their planet – attempting to tap the plants icecaps to survive (Lowell, 1906; Lowell, 1908). The idea of intelligent Martian life clinging on to a drying, dying world captured the public imagination and many novels were published on the theme of human exploration of Mars, or Martians visiting Earth, sometimes with the aim of colonising our planet to escape their own

dying world – for example H.G. Wells' novel "The War of the Worlds", first published in 1898 and since adapted into various radio broadcasts and films.

As we saw in Chapter 2 it was a contemplation of life on Mars that first inspired Lovelock to formulate the Gaia Hypothesis. During the 60's and 70's when spacecrafts reached Mars they found an icy world, devoid of any obvious signs of life, as predicted by Lovelock. With no signs of chemical disequilibrium in the Martian atmosphere he had deduced that the presence of any sort of widespread life was highly unlikely (Lovelock, 1965). However, in the past Mars may have been more hospitable to life as we know it. Evidence suggest that there once was large quantities of liquid water on the surface of Mars. This evidence comes from physical signatures of past rivers and oceans carving features onto the surface of Mars that we can see today (Carr, 1996).

If liquid water once existed in large quantities on the surface of Mars, it means the surface temperatures and pressures on Mars must have once been much closer to those found on Earth; The current pressure on Mars is so low that liquid water is unstable on the Martian surface (Heldmann et al., 2005). The current explanation is that the once thick Martian atmosphere allowed for pressures and temperatures suitable for liquid water to be present in large quantities, with the solar wind stripping away this atmosphere to the present day low levels (Jakosky et al., 1994). Mars has also had volcanic and tectonic activity over its history, and is still geologically active today (Watters and Schultz, 2010). With water and tectonic activity both being important to life and atmospheric regulation on Earth, there is a possibility that Mars was host to life in its past.

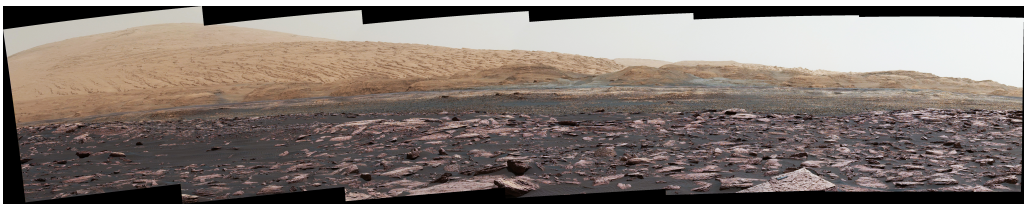


FIGURE 6.3: The surface of Mars: 'Vera Rubin Ridge' on Mount Sharp, Mars, taken by NASA's Curiosity Mars rover. We see a dry landscape with four geological layers. Image credit: NASA/JPL-Caltech/MSSS

Recent discoveries of liquid water on the surface of Mars have reignited the possibility of Martian life existing today. This liquid water however is only found occasionally as liquid brine in very small quantiles on the Martian surface in shallow soil (Ojha et al., 2015). The presence of liquid water

suggests that if Mars did once have abundant life, it is possible that it still exists in sparse pockets (Wilkinson, 2006), a possibility strengthened by the fact that we find life in the Mars-like conditions of the Antarctic dry valleys (Siebert et al., 1996). Figure 6.3 shows a part of the surface of Mars taken by NASA's Curiosity Mars rover. In contrast to Venus, machinery can last a long time on the Martian surface. Curiosity has been exploring Mars since August 2012 and is still operational (and you can follow its adventures on twitter!). By analysing Martian rocks, Curiosity found that the Martian surface was once suitable for microbial life (Squyres et al., 2008). In 2020 the Rosalind Franklin Rover (previously the ExoMars rover) will be launched to join Curiosity on Mars and search for evidence of past life (Vago et al., 2017).

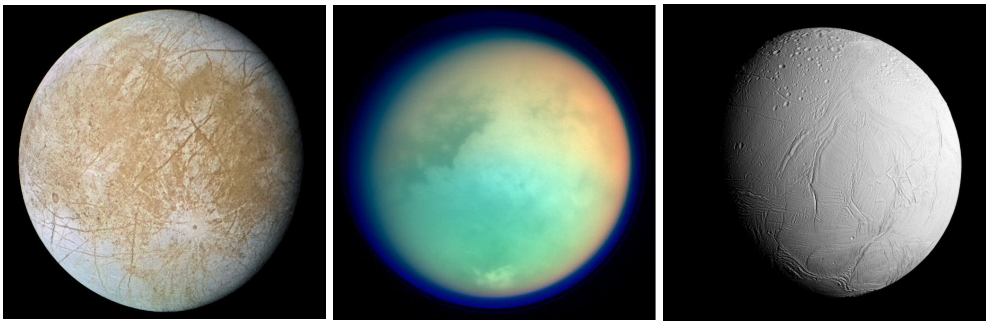
1 .3 Habitable moons?

There are a further three bodies in our solar system subject to popular interest for astrobiology, Europa, a moon of Jupiter, and Titan and Enceladus, both moons of Saturn. Europa, though much further from the sun than the Earth, is thought to have a large ocean of liquid water under a thick later of ice (Squyres et al., 1983; Carr et al., 1998). The moon is continually flexed by the tidal forces of moons orbiting Jupiter at different frequencies and this would generate enough heat to maintain liquid water (Cassen, Reynolds, and Peale, 1979; Cassen, Peale, and Reynolds, 1980; Ross and Schubert, 1987; Ojakangas and Stevenson, 1989). It is speculated that life could exist in this ocean of water (Chyba, 2000b; Chyba, 2000a; Chyba and Phillips, 2001; Chyba and Phillips, 2002). Missions are planned to land on the surface of Europa and drill down, with possible water robot missions being planned and tested in the artic waters on Earth. These robots would analyse the chemistry and geological features and check for signs of life.

Titan, although far colder than Earth with an average surface temperature of -179^{o}C is very similar to the Earth in a number of ways, including a substantial atmosphere(Lunine and Atreya, 2008b; Lunine and Atreya, 2008a; Clarke, Wannawichian, and Strobel, 2010), volcanoes and a hydrocarbon chemical cycle that mirrors the water cycle on Earth, with lakes, rivers and rain (Elachi et al., 2005; Soderblom et al., 2007). With large bodies of liquid hydrocarbons it is theorised that life could use liquid methane or ethane (McKay and Smith, 2005) as a solvent instead of water, which life on Earth uses. If such life does exist on Titan, it would be different to any life known on Earth and would likely have had an origin separate to life on Earth. This

would be strong evidence for life being common throughout the universe (Lunine, 2009).

Enceladus is an ice covered moon, with water-rich plumes which vent from the southern polar area (Hansen et al., 2006). These plumes are similar to geysers found on Earth and evidence indicates that Enceladus has a large sub-surface ocean of liquid water at its southern pole that is around 10 km thick buried under 30-40 km of ice crust (Iess et al., 2014). The geysers combined with observations of internal heat escaping, demonstrate that Enceladus is currently geologically active (Spencer et al., 2006) and in 2018, complex macromolecular organics were detected in Enceladus's plumes (Postberg et al., 2018). The presence of an ocean with hydrothermal activity makes Enceladus a good potential host of alien life (Parkinson et al., 2008; Spencer et al., 2009; McKay et al., 2014).



(A) Europa (B) Titan (C) Enceladus

FIGURE 6.4: Europa a moon of Jupiter and Titan and Enceladus, moons of Saturn, are also the source of speculation for hosting extraterrestrial life. Image credit: NASA

1 .4 Lithopanspermia

Lithopanspermia is the hypothesis that life could be transported between planets within rocks dislodged from their planet of origin via natural impacts (Nicholson, 2009). It is a development of the panspermia hypothesis that has been debated for at least 2 millennia (Kamminga, 1982). Lithopanspermia is currently considered to be a viable hypothesis, although whether it has ever occurred is unknown. Recent experimental and observational developments on how life survives within rocks and their resistance to extreme conditions (Horneck, Klaus, and Mancinelli, 2010; Meyer et al., 2011), coupled with our understanding on solar system impact dynamics (Reyes-Ruiz et al., 2012), suggests that it is possible for life to travel between planet in the same solar

system (Mendonça, 2014), and possibly even beyond (Valtonen et al., 2008; Belbruno et al., 2012).

If such events can occur and have occurred it has obvious implications for the search for alien life. If life need not emerge on a suitable planet, but could also be transported to a suitable planet, it increases the chances of life in the universe. Within our own solar system as Venus, Earth and Mars are all thought to have hosted habitable surface conditions at the same time, it's possible that life originating on Earth might have colonised Mars or Venus, or that life on Earth didn't originate on Earth at all. The rapid appearance of life on Earth after habitable conditions are thought to have formed is taken by some as evidence for life having non-Earthly origins (Nicholson, 2009). Lithopanspermia has also been suggested as providing a refuge for microorganisms during sterilising impacts (Sleep and Zahnle, 1998). In these cases the sterilising impact would blast microbe-bearing rocks into space, and some of these rocks would lack the velocity to escape the planet's gravity. They may then settle into decaying orbits until finally falling back to the planet some time later and possibly after conditions on the planet are habitable once more, thus in effect 'reseeding' the planet. Any possibility of lithopanspermia would increase the probability of finding alien life.

2 Defining the 'Habitable Zone'

Before I go on to discuss planets outside of our solar system, I will first explain a criteria that is useful for classifying exoplanets – the Habitable zone.

When looking at planets and moons beyond our solar system we cannot see such fine detail as we can with Venus or Enceladus as currently, visiting is not a feasible option. Therefore a more general approach is used to determine whether a planet is possibly habitable or not, and this criteria depends largely on the size of the planet, the spectral class of the planet's host sun, and the distance the planet is from its sun.

Specifications for what makes a habitable planet are usually based on the conditions we see on Earth as life is clearly abundant on this planet and the Earth hosts the only life we know of. The process for determining the habitable zone around a star has been done in many ways, however the most common is to assume an Earth like planet, and 'move' the planet into the sun until runaway greenhouse and ocean boiling takes place, as a measure of the inner limit to habitability, and shifting the planet outwards until global freezing occurs to determine the outer edge of the habitable zone (Hart, 1979).

Current estimates for the habitable zone of our own solar system are 0.99 AU - 1.70 AU (Kopparapu et al., 2013). This places the Earth just inside the habitable zone today. Mars also lies within this habitable zone, but the potentially habitable moons Europa, Titan, and Enceladus lie far outside it. Estimates for planets differing to Earth change the bounds of the habitable zone, for example dry planets might have habitable zones far closer to their host star (Abe et al., 2011), whereas planets with thick insulating hydrogen atmospheres might extend the habitable zone outwards (Pierrehumbert and Gaidos, 2011).

What is traditionally neglected from these models is a biotic response to changing conditions. As a star ages, its luminosity changes thus altering the habitable zone around the planet. Planets that were once in the habitable zone might move beyond it as solar conditions change. Life on a planet undergoing external forcing will react – even death is a reaction to a change. This life response could act to regulate conditions on the planet and thus maintain habitability. Therefore the Gaia hypothesis has implications for determining what constitutes a habitable planet.

Should life one day be discovered say within Enceladus's deep oceans, it will change how we understand habitability. However for the purposes of remote observation of distant solar systems, a general rule for potential habitability of a planet or moon is useful, and any life in sub-ice ocean worlds like Enceladus would be very difficult to observe without robotic exploration missions. Worlds similar to Earth, with gaseous atmospheres can have their atmospheric chemical components measured via transit spectroscopy, as the planet, or moon, transits in front of its sun (with respect to our point of view on Earth) (Charbonneau et al., 2002), and direct detection of light emitted by exoplanets (Charbonneau et al., 2005).

With limited resources a habitable zone definition also helps to narrow down candidates for analysing to only those with a good chance of hosting life as we know it. If life interacts strongly with its host planet to change atmospheric compositions, this will have an impact on our definition of a habitable zone and can help inform where to focus our search for inhabited exoplanets.

3 Exoplanets

Models and hypotheses are highly useful tools but without real data to apply them to, they can only take us so far. To answer the question of how rare

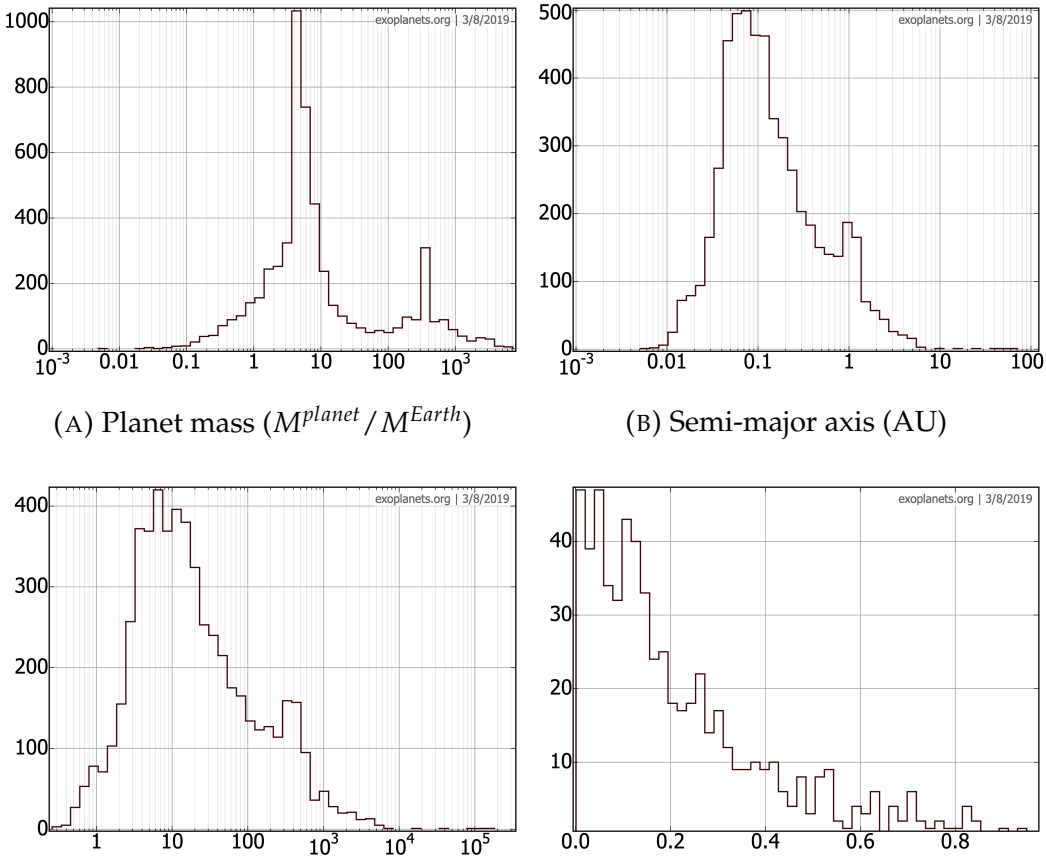
Earth might be, or whether we are alone in the universe, we need data of other worlds orbiting other stars – exoplanets.

To date 4071 planets have been found in 3043 planetary systems with 659 of those being multiple planet systems (see exoplanet.eu/catalog). The Kepler telescope launched in March 7, 2009 detects the present of exoplanets by searching for periodic dimming of star luminosities caused by the transit of planets (Borucki et al., 2010; Koch et al., 2010), and the James Webb Space telescope, currently due to be launched in March 2021, will allow us to analyse the atmospheres of other planets in more detail than ever before (Gardner et al., 2006; Beichman et al., 2014), and potentially search for bio-signatures (Seager, 2014; Seager, Bains, and Petkowski, 2016).

The various techniques for finding exoplanets come with certain observational biases. The radial-velocity technique uses changes in the radial velocity of a star along its orbit and centre of mass to infer the presence of orbiting planets. The closer or larger the planet, the larger the amplitude of the variation of the stellar velocity meaning that planets that are larger or closer to their host star are easier to identify using this method (Udry and Santos, 2007). A similar bias is present using the transit method of exoplanet observation which involves observing small regular reductions in the luminosity of a star which indicate that an object is transiting between the star and our line of sight. The closer to its host star a planet is, the more likely a transit is to occur (Burrows, 2014). The transit method has been used to discover the majority of known exoplanets to date, therefore that the majority of known exoplanets are either significantly larger than Earth and/or orbit their host stars far closer than Earth does is at least partially a product of observational bias. Figure 6.5 shows a summary of some of the properties of exoplanets found to date.

Figure 6.6 shows histograms of data on stars known to host exoplanets, and shows their mass and their Fe/H ratio with respect to our sun's. These figures show that many stars similar to our own are host to exoplanets. Understanding the properties of stars hosting exoplanets is important when considering alien life as, for example photosynthesis could be different on a planet orbiting a star of a different spectral type to our own (O'Malley-James et al., 2012), and iron is key to life as we know it (Kroneck and Torres, 2015).

A detailed summary of possibly habitable (as we understand it) exoplanet findings as of 2014 from Seager (2014) is shown in Figure 6.7 and shows the number of planets with masses less than 10 Earth masses that have been detected in the habitable zone, for both the traditionally defined habitable zone



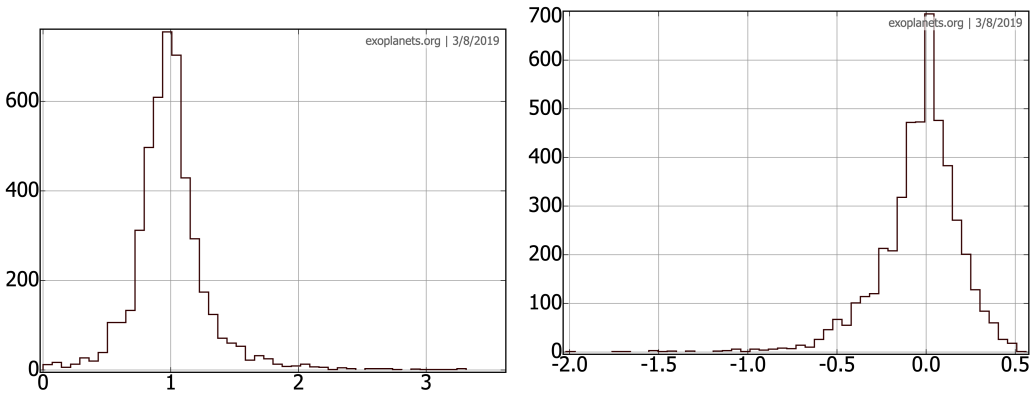
(A) Planet mass (M^{planet} / M^{Earth})

(B) Semi-major axis (AU)

(C) Orbital period (days)

(D) Orbital eccentricity

FIGURE 6.5: Histograms generated at exoplanet.org of the latest exoplanet data showing the abundance of various planet properties. We see that the majority of exoplanets found are of order of a few Earths in terms of mass, and orbit their host starts far closer, and far more rapidly than the Earth does our sun. The eccentricity of most exoplanets identified is low (close to circular). Earth's eccentricity is ≈ 0.017.



(A) Mass of host star (w.r.t. solar mass)

(B) Fe/H ratio on log scale relative to our sun (0 is solar, -1 is 1/10th of solar abundance)

FIGURE 6.6: Histograms generated at exoplanet.org of the latest exoplanet data showing properties stars known to host planets. In both cases these are shown relative to these properties of our Sun.

and the zone extended in either direction for planets that differ to Earth (dry planets closer to the sun and hydrogen rich planets further out).

Exciting candidates for further investigation have already been identified, for example the 7 Earth-sized planets orbiting the dwarf star TRAPPIST-1 (Gillon et al., 2016; Gillon et al., 2017), see Figure 6.8. It is thought that liquid water might be possible on the surface of some of these planets (Kopparapu et al., 2013; Leconte et al., 2013), and as they transit their host star, it will be possible to perform in-depth studies of their atmospheric properties (Wit et al., 2016; Barstow and Irwin, 2016).

The building blocks for life as we know it are abundant in the universe. Amino acids have been found in molecular gas clouds in space (Sorrell, 2001), perhaps making the origin of life appear to be not as rare as once thought (although there are many steps along the way from animo acids to life). If the recipe for life is abundant in the universe why have we not yet found a universe teeming with life? It could be that the Earth is exceedingly rare, with just a right properties to host life for long time periods. However as our telescope technology advances, astronomers have been finding thousands of exoplanets, with many in the habitable zone, as we currently understand it, and of similar sizes to Earth (Cassan et al., 2012; Petigura, Howard, and Marcy, 2013). Based on data from the Kepler telescope, astronomers estimate that 22% of Sun-like stars have Earth-sized planets orbiting within their habitable zone (Petigura, Howard, and Marcy, 2013). Even if Earth like conditions vital for life, the more exoplanets we find, the more it seems that our solar system

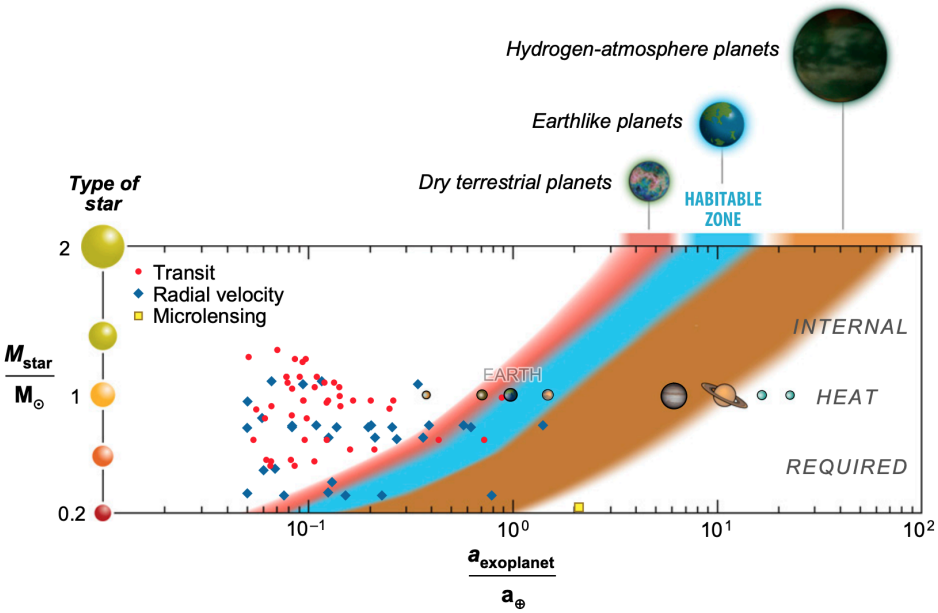


FIGURE 6.7: Diagram from Seager (2014) (adapted from Seager (2013)) showing the number of known planets with a mass less than 10 Earth masses (data from (Rein, 2012)) plotted against the distance from their host sun (relative to Earth's orbital radius) (x-axis), and their mass relative to Earth's (y-axis). Blue shows the traditional habitable zone for $N_2 - CO_2 - H_2O$ atmospheres (Kasting, Whitmire, and Reynolds, 1993; Kasting et al., 2014). Dark pink shows the inward extended habitable zone for dry planets (Zsom et al., 2013; Abe et al., 2011) and orange the outwards extended habitable zone for hydrogen-rich atmospheres (Pierrehumbert and Gaidos, 2011). Our solar system's planets are shown with images for reference.

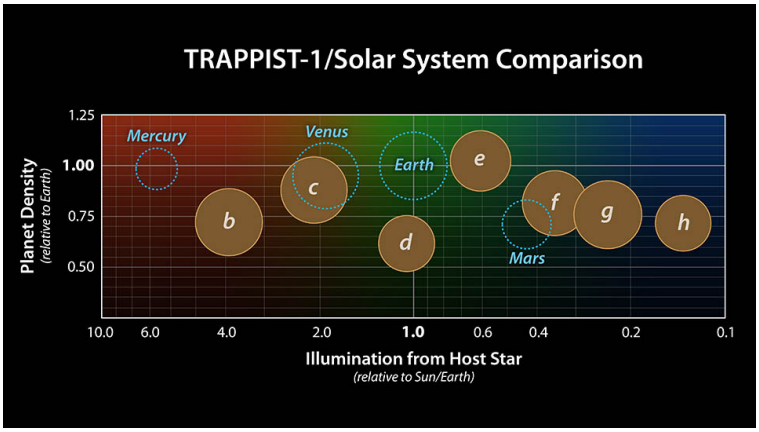


FIGURE 6.8: The Trappist-1 system compared to our solar system. Image Credit: NASA/JPL-Caltech

is not unique at all. Estimates by Frank et al. (2001) based on the Drake equation predict the existence of around half a million Gaias in the Milky Way alone.

Soon, when the James Webb telescope mission is fully operational we will be able to look into the atmospheres of planets lightyears away from us and determine their chemical composition. If we find planets with atmospheres in chemical disequilibrium, as is the case here on Earth, it might be the first sign that we are not alone after all.

4 A Gaian Bottleneck

We have seen that in the past Venus was cool enough, and Mars was warm enough, for both planets to have liquid water oceans present on their surfaces, something not present on either today. The increasing luminosity of the Sun is thought to have caused a runaway greenhouse effect on Venus, leading to the oceans boiling away and the current scorching conditions on Venus. Meanwhile solar wind is thought to be responsible for stripping the Martian atmosphere and reducing surface temperatures and pressures to where liquid water can no longer be supported on the surface. These dramatic changes on both planets pushed them away from conditions that might have once been habitable to Earth-like life, to conditions that are now almost certainly hostile. We could look at the differences between the histories, solar locations, and the present day conditions of Venus, Earth and Mars and subscribe to purely geological and astronomical explanations for them. However what if life plays a role in determining the long term habitability of a planet?

The concept of Gaia having ramifications for planet habitability has been explored before; the theory of Gaian bottlenecks (Chopra and Lineweaver, 2016) suggests that early in a planet's history, assuming initially habitable conditions, life must quickly establish self regulating feedback loops in order to maintain habitable conditions. If it fails, life goes extinct and leaves the planet in a lifeless state. With the building blocks of life being so abundant in the universe, and the discovery that planetary systems similar to our solar system are common, authors Chopra and Lineweaver postulate that the apparent scarcity of life might be explained by considering how life interacts with its host planet. Chopra and Lineweaver (2016) postulate that 'seeding' life, or life arising, on a planet is a common event in the universe. Although we have not been yet able to create synthetic life, there is strong evidence that

life appeared on Earth as soon as conditions allowed (see Section 1) implying that the emergence of life on a planet might not be as tricky as traditionally thought.

Chopra and Lineweaver (2016) suggest that the emergence of self-regulation is the tricky part in forming a planet suited to long-term habitability. They suggest that while the emergence of life might be common, that this life must evolve quickly to form recycling loops for nutrients and insert itself into the planet's abiotic processes sufficiently to perform self-regulation on a planetary scale. If life fails, life on the planet becomes extinct, but if life succeeds, then the planet can enjoy long term habitability. The authors refer to this phenomena as a 'Gaian-bottleneck'; they postulate that the establishment of a self-regulating biosphere is an essential step in the formation of a inhabited planet, and that this step might be be difficult for early life to achieve fast enough to avoid extinction. This theory of Gaian bottlenecks could be linked to recent models of bifurcations in early planet formation (Lenardic, Crowley, and Weller, 2016).

The formation of plate tectonics on a planet is temperature dependent and simulations by Lenardic, Crowley, and Weller (2016) show that there might be two alternate stable states for Earth-sized rocky planets – a state with or a state without plate tectonics, for the same temperature (Weller, Lenardic, and O'Neill, 2015; Weller and Lenardic, 2018). As plate tectonics are important on Earth for climate regulation, this could have profound impacts on the habitability of a planet. Lenardic, Crowley, and Weller (2016) suggest that Earth and Venus could represent two different stable states for the same system and predict that small fluctuations early in a planet's history could determine the end state of that planet, with life possibly providing such a perturbation. Research showing that life could impact the mantle dynamics of a planet (Höning et al., 2014) lends further support to this hypothesis.

We could conceive of a thought experiment where we rewind our solar system back in time, and set the clock running again, back when both Earth and Venus had surface liquid water. Would we get the same result again? A scorching Venus and an idyllic Earth, or could Venus have become the host of abundant life while Earth suffered runaway heating as the Earth's biosphere failed to establish regulatory feedback loops? Clearly this experiment is impossible, however by observing solar systems beyond our own we might find answers. Should a planet in a similar position in its solar system to Venus be found to have signs of life it will change our understanding of planetary habitability.

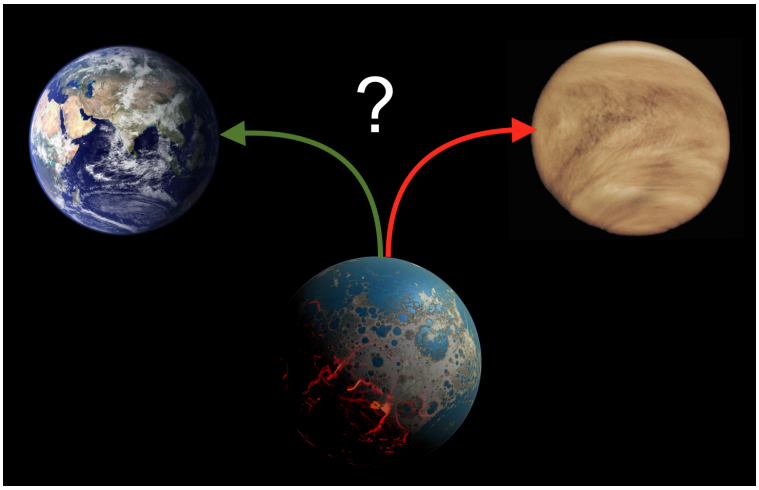


FIGURE 6.9: Are Earth and Venus alternate states of the same system? Image of a young Earth-like planet evolving into two possible states – Earth or Venus. Image Credit: NASA/JPL-Caltech

5 Summary

In this chapter I have given a brief overview on the possible habitability of several objects within our solar system, and where current understanding lies with the concepts of habitable zones and the detection of potentially habitable planets. Venus in particular is of great interest with respects to our understanding of our own planet as it is so similar in size, mass, and composition. Could Venus show how Earth would look today had early life failed to have become established? Or more excitingly, if life had become established on early Venus, would Venus today look more like Earth? Was a Venusian Gaia possible?

The next Section of this thesis further explores these themes in a new model of environmental regulation by evolving biospheres called the Exo-Gaia model.

Chapter 7

The ExoGaia Model

This chapter explores a new model called the ExoGaia model. ExoGaia builds from previous Gaian models and is heavily based on the Flask model (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010; Nicholson et al., 2017), with elements of the Greenhouse world model (Worden, 2010; Worden and Levin, 2011). It considers the regulation of an atmosphere to regulate a global temperature instead of an independent temperature parameter to regulate as in previous flask models (see Section 2 .2). A familiar regulation mechanism emerges in the ExoGaia model, however the model exhibits behaviours not before documented in Gaian models. The results from ExoGaia has implications for exobiology, our search for inhabitable / inhabited planets, and also considers the alternative histories our planet might have had, and the possible futures before us.

Whereas in the majority of the Flask models, including the version explored in Chapter 4, the impact microbes have on their global temperature is independent of the specific nutrients they consume and excrete, ExoGaia is inspired by considering life's interaction with the atmosphere on Earth. Plant life takes in CO_2 as part of its metabolism, and as CO_2 is a greenhouse gas, this impacts our planetary temperatures. Therefore what life removes / inputs to the atmosphere will impact global temperatures and so this is mimicked in ExoGaia by having microbes interact with a very simple planetary atmosphere on a planet with simplistic geochemical cycling.

ExoGaia also differs from the previous Flask models as life now must 'catch' a narrow window of habitability as its planet is evolving, and then maintain that habitability. Most model planets, in the absence of life, would quickly revert to a highly inhospitable state, however if life appears it can often regulate the atmosphere of its host planet and maintain habitable conditions. The underlying geochemistry of the model planets proves to be very

important in how successful life is in firstly colonising the planet, and secondly in maintaining habitability for long time spans. This model demonstrates 'Gaian bottlenecks' first described by Chopra and Lineweaver (2016). A 'Gaian bottleneck' is where, for the same model planet, life either quickly establishes regulatory feedback loops causing the planet to remain habitable for significant time periods, or life does not act fast enough and the planet reverts to an inhospitable state and all life goes extinct.

The work presented in this chapter has been published in the Monthly Notices of the Royal Astronomical Society, June 2018, titled "Gaian bottlenecks and planetary habitability maintained by evolving model biospheres: the ExoGaia model" (Nicholson et al., 2018). I was the lead author on this paper. My contributions to the published work include forming the initial concept for the ExoGaia model, writing the code used to generate the data contained within the paper, analysing the data, creating the graphs and writing the bulk of the text. The words and images in this work is presented as it was published, with only minor typos as changes from the original manuscript and taken out of the journal template.

Gaian bottlenecks and planetary habitability maintained by evolving model biospheres: the ExoGaia model

Arwen E. Nicholson, David M. Wilkinson, Hywel T.P. Williams and Timothy M. Lenton

Abstract

The search for habitable exoplanets inspires the question – how do habitable planets form? Planet habitability models traditionally focus on abiotic processes and neglect a biotic response to changing conditions on an inhabited planet. The Gaia hypothesis postulates that life influences the Earth's feedback mechanisms to form a self-regulating system, and hence that life can maintain habitable conditions on its host planet. If life has a strong influence, it will have a role in determining a planet's habitability over time. We present the ExoGaia model – a model of simple 'planets' host to evolving microbial biospheres. Microbes interact with their host planet via consumption and excretion of atmospheric chemicals. Model planets orbit a 'star' which provides incoming radiation, and atmospheric chemicals have either an albedo, or a heat-trapping property. Planetary temperatures can therefore be altered by microbes via their metabolisms. We seed multiple model planets with life while their atmospheres are still forming and find that the microbial biospheres are, under suitable conditions, generally able to prevent the host planets from reaching inhospitable temperatures, as would happen on a lifeless planet. We find that the underlying geochemistry plays a strong role in determining long-term habitability prospects of a planet. We find five distinct classes of model planets, including clear examples of 'Gaian bottlenecks' – a phenomenon whereby life either rapidly goes extinct leaving an inhospitable planet, or survives indefinitely maintaining planetary habitability. These results suggest that life might play a crucial role in determining the long-term habitability of planets.

1 Introduction

Most models of habitable planets and the boundaries of the habitable zone focus on the physical processes happening on planets to determine the limits of habitability (for example (Cockell, 2007) and (Kopparapu et al., 2013)). These models neglect a biotic response to changing conditions on an inhabited planet. The Gaia hypothesis postulates that life influences the Earth's feedback mechanisms to form a self regulating system (Lovelock and Margulis, 1974; Lenton, 1998; Lovelock, 2000). We see the signature of life on our planet in the chemical composition of our atmosphere, oceans, and soil. If life has a large effect on its host planet, this has implications for habitable exoplanet research. One area where the Gaia hypothesis has relevance for exoplanet research is around the establishment of life on a previously uninhabited planet. The idea of Gaian bottlenecks (Chopra and Lineweaver, 2016) suggests that early in a planet's history, assuming initially habitable conditions, life must quickly establish self regulating feedback loops in order to maintain habitable conditions. If it fails, life goes extinct and leaves the planet in a lifeless state. Gaian bottlenecks could be linked to recent models of bifurcations in early planet formation (Lenardic, Crowley, and Weller, 2016).

Lenardic, Crowley, and Weller (2016) suggest that the end state of a planet is not entirely deterministic. Plate tectonics, key to climate regulation, are affected by the temperature of the planet. To demonstrate this, Lenardic et. al. simulate a planet with plate tectonics, heat the planet until the tectonics disintegrate and then cool the planet back to its original temperature. After cooling, the plate tectonics are not reformed, suggesting that there are two stable states for the same temperature. Venus and Earth are traditionally thought to be different classes of planet – although similar in size, mass and chemical composition, Venus's closer orbit to the Sun is thought to have doomed it to its current state. However, evidence suggests that Venus once hosted large bodies of water (Donahue et al., 1982; Jones and Pickering, 2003), which since boiled away in a runaway greenhouse effect (Kasting, 1988), leading to present day surface temperatures of over 400^{o}C. Lenardic et. al. suggest that Earth and Venus could represent two different stable states for the same system. They predict that small fluctuations early in a planet's history could determine the end state of that planet, with life possibly providing such a perturbation. Earth is very different from what it would be if it were uninhabited. Our atmosphere would be dominated by CO_2 as is the case on

Venus and Mars and this would affect the Earth's surface temperature. If Venus once had life back when it had water, could we be on the lucky side of a Gaian bottleneck? While most models place Venus outside the habitable zone as Venus receives almost twice the amount of solar radiation as Earth, a few allow the potential for a habitable Venus today (e.g. (Zsom et al., 2013) and (Yang et al., 2014)). Recent models (Yang et al., 2014; Way et al., 2016) demonstrate the important role planetary rotation and topography play in understanding a planet's climatic history, and suggest that rocky planets that retain significant water after formation can experience habitable conditions well within the traditionally defined inner edge of the habitable zone (e.g (Kopparapu et al., 2013)).

Inspired by these important questions, we present a new abstract model of environmental regulation performed by evolving biospheres – the Exo-Gaia model. We model simple 'planets' with atmospheres whose chemical composition influences planetary temperatures. Model microbes consume and excrete atmospheric chemicals, via temperature dependant metabolisms. Thus microbes can impact planetary temperatures by altering the chemical composition of their host planet's atmosphere. We investigate whether a simple biosphere can regulate its host planet's temperature within habitable bounds. We focus on a biotic response to planetary conditions, in contrast to most habitability models. We do not attempt to model the complexities of real planets, allowing us to isolate purely biotic phenomena emerging from the model. As most models of planetary habitability focus on abiotic phenomena alone, future work should combine these abiotic models, with a biotic model such as ExoGaia to investigate the impact of adding biotic feedback.

We will use real world language such as 'planet' and 'temperature' when discussing ExoGaia as the model is inspired by real world questions. However, ExoGaia is not intended to be a realistic model of planetary formation or dynamics; ExoGaia is an abstract model of a thought experiment (Paolo et al., 2000), in line with e.g. Daisyworld (Watson and Lovelock, 1983) that can be used to generate hypotheses about real planets – can a biosphere perform planetary regulation? Do Gaian bottlenecks occur?

This work builds on previous Gaian model research. There is a large body of literature on the Gaia hypothesis and on the many models used to investigate this hypothesis and so an in-depth review of Gaia will not be given here but the reader is pointed to (Boston and Schneider, 1993; Lovelock, 2000;

Schneider et al., 2013) for background on the Gaia hypothesis, and (Downing and Zvirinsky, 1999; Wood et al., 2008; McDonald-Gibson et al., 2008; Williams and Lenton, 2010; Dyke and Weaver, 2013; Nicholson et al., 2017; Arthur and Nicholson, 2017) for an overview of some key Gaian models investigated to date.

2 ExoGaia Model Description

ExoGaia is heavily based on the 'Flask' models (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010; Nicholson et al., 2017), and shares similarities with the 'Greenhouse world' model (Worden, 2010; Worden and Levin, 2011). We will first describe the model, then point out the key similarities and differences between these models and ExoGaia. An in depth model description is given in Appendix A.

2 .1 Model outline

We model simple 'planets' with well-mixed planetary atmospheres, the composition of which influences planetary temperatures. These planets are host to microbial life that consume and excrete atmospheric chemicals. All planets orbit a 'star' that provides incoming radiation. We use the following terminology to describe ExoGaia:

- Chemical – a particular chemical species. Each chemical has either a cooling (e.g. reflective, high albedo) or warming (e.g. insulating) effect on the atmosphere.
- Chemical Set – as the set of chemical species present in the system.
- Geochemistry – the static network of geochemical links between chemical species, i.e. the abiotic processes.
- Connectivity – the probability of any two chemical species in a chemical set being connected by a geochemical process (also referred to as a link or connection).
- Planet – a system with a unique chemical set and geochemistry combination.
- Biochemistry – the biological links created by microbe metabolisms forming the biochemical network. Unlike the geochemistry of a planet, the

biochemistry is not fixed; it evolves as a function of microbial evolutionary and ecological dynamics.

- Abiotic Temperature ($T_{abiotic}$) – the temperature of a planet without life when its atmosphere is in equilibrium. Most of our simulated planets have abiotic temperatures that are inhospitable to life. (For the results presented in this paper the majority of simulated planets (over 70%) have inhospitably high abiotic temperatures. Appendix B explores alternative scenarios).

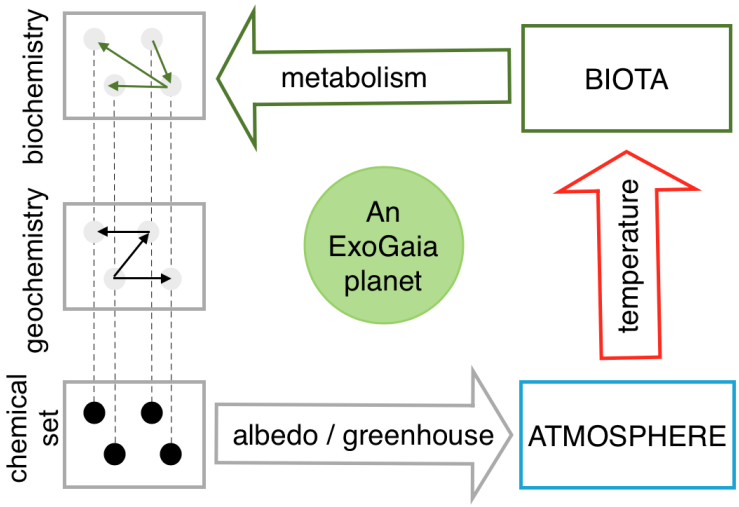


FIGURE 7.1: The ExoGaia model schematic. Circles represent chemical species and arrows represent the geochemical or biochemical links between them.

Figure 7.1 shows a schematic for the ExoGaia model illustrating how each part of the planet – the chemistry, geochemistry and biochemistry are connected. We use agent based dynamics to model our ExoGaia experiments and therefore time is represented in model 'timesteps'.

2 .2 Microbes

Model microbes consume and excrete atmospheric chemicals. Microbe metabolisms are genetically encoded and assume an external energy source, i.e. a star. The temperature of the host planet, T_{planet}, affects microbe metabolisms, and for simplicity all microbes share the same temperature preference, T_{pref}. At $T_{planet} = T_{pref}$ microbial growth rates will be at the maximum. As T_{planet} moves away from T_{pref} the microbes' consumption rate decreases and the

growth rate drops. If the difference between T_{pref} and T_{planet} is too large, microbes will be unable to metabolise and will not consume/excrete any chemicals. Microbes die if their biomass drops below a certain threshold and there is also a constant probability of random death. If a microbe's biomass reaches the reproduction threshold it reproduces asexually, with a constant probability of mutation for each gene, allowing new species to evolve on planets.

2 .3 Chemicals

Model planet atmospheres are composed of various 'chemical species'. There is a large body of literature on chemical reaction network theory (Feinberg, 1987) which models the behaviour of real world systems and has been applied to planetary atmospheres, e.g. Solé and Munteanu (2004). We use a very simple chemical reaction network in ExoGaia.

Each chemical species has an insulating or a reflective property. We simplify real chemistry and limit a chemical species to being either insulating or reflecting, but not both. We can also take this simplification to be the overall impact a chemical has on the atmosphere. The collection of chemical species (and their greenhouse / albedo properties) possible on an ExoGaia planet is referred to as a 'chemical set'. Not all chemical species in a chemical set might be present on a model planet. For a chemical species to be present it must be created by some process. The processes by which a chemical species can be created (or destroyed) are covered in later Sections on "Atmosphere", "Geochemistry" and "Biochemistry".

All model atmospheric chemicals are assumed to be gaseous. Realistic atmospheric gases have both insulating and reflecting properties (via absorption and Rayleigh scattering) with the net effect depending on the abundance of the gas, the overall atmospheric mass (Wordsworth and Pierrehumbert, 2013), and the spectral energy of the host star (Kaltenegger and Sasselov, 2011). In the ExoGaia model only the abundance of the gas determines it's overall impact on the host planet. In realistic scenarios, the outer edge of the Habitable zone depends on the limit where the condensation and scattering caused by adding more CO_2 to an atmosphere outweighs its greenhouse effect (Kopparapu et al., 2013).

2 .4 Temperature

We use a linear approximation of the Stefan-Boltzmann law when calculating T_{planet}. This simplification has been shown to not greatly change the overall

behaviour of the Daisyworld model (Watson and Lovelock, 1983; Saunders, 1994; De Gregorio, Pielke, and Dalu, 1992; Weber, 2001; Wood, Ackland, and Lenton, 2006; Wood et al., 2008). The Stefan-Boltzmann equation is close to linear at real world habitable temperatures, i.e. near 22^oC. In ExoGaia, we are only interested in planetary dynamics when there is life on a planet, so while the 'temperature' in the ExoGaia model is not constrained, we are only interested in a narrow range of habitable temperatures. The temperature behaviour outside this range is not important to the results. We will be using an unrealistic T_{pref} for our model microbes to highlight the abstract nature of the model, however as a near linear relationship exists at habitable conditions on Earth, and we are striving to simplify the model abiotic environment as much as possible, we use a linearised Stefan-Boltzmann law in our model and take $\beta \propto T$, where β is the energy provided to the planet by the host star per timestep and T is temperature. We then make a further simplification and take the value of β to be equal to the value of T. Appendix B4 further explores this temperature simplification.

2 .5 Atmosphere

Many real planets have (or had), for example, volcanoes that spew forth aerosols and gases which come from the crust and the mantle. Gases can be lost from the planet's atmosphere by processes such as sublimation or some gases (e.g. hydrogen) can be lost to space. We abstract these processes in the ExoGaia model.

All model planets start with an 'empty' atmosphere, and a constant inflow of chemicals from an external source begins at the start of each experiment. The 'source chemicals' are the subset of chemical species in the chemical set that experience this inflow. Non-source chemicals do not exist on a planet unless created via a geochemical or biochemical process. There is a constant rate of atmospheric chemical outflow, performed by removing a fixed percentage of the well-mixed atmosphere each timestep. There is no spatial structure in the model.

A planet's atmospheric composition influences T_{planet}. We define A_I as the fraction of the planet's current thermal energy retained by the atmosphere via insulation, and A_R as the fraction of incoming radiation reflected by the atmosphere. Using the simplification described in Section 2 .4, the value of β_{planet} is the value of T_{planet}. Therefore $(1 - A_I)\beta_{planet}$ is equivalent to a planet's temperature decrease due to energy radiation into space, where

β_{planet} is the thermal energy of the planet. Similarly, $(1 - A_R)\beta_{star}$ is equivalent to the increase in temperature due to incoming solar radiation, where β_{star} is the incoming solar radiation to a planet per timestep. Therefore a stable temperature is achieved if:

$$(1 - A_I)\beta_{planet} = (1 - A_R)\beta_{star} \tag{7.1}$$

The values of A_I and A_R depend on the chemical composition of the atmosphere, and exist in the range $[0, 1]$. This relation is described in an equation in Appendix A. We calculate β_{update}, the updated thermal energy of a planet including the insulating and reflecting effect of the atmosphere, in the following way:

$$\beta_{update} = A_I\beta_{planet} + (1 - A_R)\beta_{star} \tag{7.2}$$

We neglect to model the complexities of atmospheric absorption in ExoGaia as that level of realism is unnecessary given the abstract simplified nature of the model. We also see that each timestep:

$$\beta_{lost} = (1 - A_I)\beta_{planet} + A_R\beta_{star} \tag{7.3}$$

of energy is lost to space either as radiation from the planet or as reflected solar radiation. Although real stars age and change in luminosity, we keep our model simple and keep β_{star} constant, to investigate the habitability of planets without external perturbation. This also makes sense biologically when considering the generation length of a microbe. It would take very, very many generations of microbes for a star to alter its solar radiation in a significant way.

If $A_I = 1$, a planet will perfectly insulate, and if $A_R = 1$ a planet will perfectly reflect all incoming radiation. Neither of these extremes is physically realistic; no atmosphere can perfectly insulate, nor reflect all incoming radiation, however this approach was favoured over choosing an arbitrary cut-off value. We are interested in regulation on habitable planets and in our experiments, the probability of T_{planet} equalling T_{stable}, the temperature required for a stable microbe population, at these limits is extremely unlikely. Taking Equation 7.1, if $A_I = 1$, then $A_R = 1$ must also be true for a constant T_{planet}. For long-term habitability, $A_R = A_I = 1$ must occur when $T_{planet} = T_{stable}$. This is highly unlikely and this scenario was not found to have happened in the results presented in this paper. Therefore this simplification does not impact on the conclusions drawn from our model.

2 .6 Geochemistry

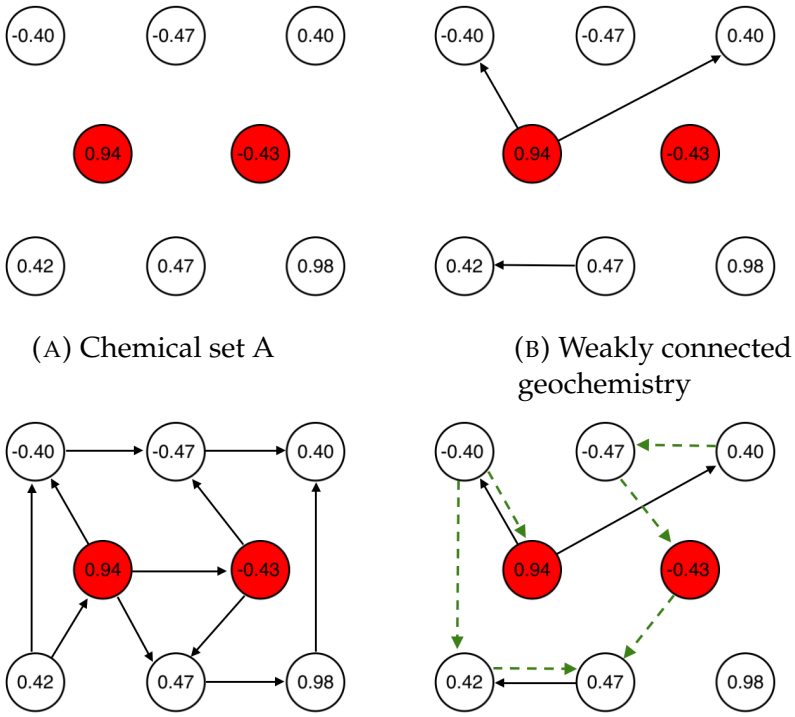
Geological links, or reactions, represent geological activity and take the form of $A \rightarrow B$, where A and B are different chemical species. This is a simplification of real chemistry where multiple reactants come together to form multiple products. Keeping the geological reactions simple allows us to more easily track chemicals through the system as they are converted via geological processes.

Geochemical links are generated based on a connectivity parameter C, which has a value between $[0, 1]$. $C = 0.2$ would determine a 20% probability for any pair of chemical species to be connected by a geochemical process. The direction of the link connection determines which direction a process take place, i.e. $A \rightarrow B$ or $B \rightarrow A$. We limit geological processes to acting in only one direction, i.e. if $A \rightarrow B$ then $B \rightarrow A$ is not allowed. We therefore describe only the net movement of chemicals linked by a geological process. The direction of a process has equal probability of acting in either direction. The link 'strength' determines how strong a geological process / reaction is, and is taken from the range $[0, 1]$. A link strength of $L = 0.3$ in the direction A $\rightarrow$ B would mean that per timestep, 30% of the particles of chemical A would be converted into chemical B. Figure 7.2 depicts two different geochemistries. As chemical abundances change, the rate of a geological process will change. E.g. a geological process of the type A $\rightarrow$ B will happen at a faster rate when chemical A is abundant compared to when it is scarce.

Geochemical links are not temperature dependant and remain constant throughout each experiment, therefore there are no geochemical temperature feedback loops in ExoGaia. Although many real world processes, e.g. silicate weathering, are temperature dependant, to isolate regulating effects caused by the microbes we remove this aspect from our model. This allows us to be confident that any regulation emerging in ExoGaia is due to the actions of the biosphere. This simplification does however limit the realism of the model and thus limit its applicability to real planets.

2 .7 Biochemistry

Model microbes form temperature dependant biochemical links via their metabolisms, e.g. a species that consumes chemical A and excretes chemical B forms the biochemical link: $A \rightarrow B$. The strength of a biochemical link depends on the number of microbe with the corresponding metabolism. Unlike the geochemical network, the biochemical network is not static; Biochemical



(A) Chemical set A

(B) Weakly connected geochemistry

(C) Highly connected geochemistry

(D) Example biochemistry

FIGURE 7.2: Geochemical and biochemical networks. Circles represent chemical species. The number inside each chemical species is its greenhouse (positive) or albedo (negative) property. Red circles are source chemicals; they have an influx from outside the system. Black solid arrows represent the geochemical links between chemical species. Green dashed lines represent biochemical links caused by microbes' metabolisms. The size of the circle does not represent the abundance of a chemical species; if a chemical species is not a source chemical nor has any geochemical or biochemical processes producing it, it has an abundance of zero.

links can change in strength, appear, and disappear, over time as the microbe community changes. Biochemical links can act in both directions, e.g. the biochemical links $A \rightarrow B$ and $B \rightarrow A$ are allowed to exist simultaneously. An example biochemistry is depicted in Figure 7.2. These microbe metabolisms are highly simplified having only a single chemical reactant and single chemical product. Real microbe metabolism are more complex with multiple reactants and products. Using simplified microbe metabolisms allows for easier tracking of chemicals around ExoGaia systems, and makes the network diagrams presented later in this paper easier to produce and interpretable. Versions of the Flask model, on which ExoGaia is heavily based, have explored more complex microbe metabolisms with abiotic environmental regulation

remaining a feature of these models (Williams and Lenton, 2008) (Nicholson et al., 2017).

The outflow of chemicals from the atmosphere is kept low, such that the timescale for a chemical to completely leave the atmosphere once produced by microbial activity is far longer than the typical lifespan of a microbe. This decouples the selection on individuals from their environmental effects and allows for long-term consequences (when compared to the average lifespan of a microbe) to occur from microbe activity. One real world example of this is the time it would take for our atmosphere on Earth to lose most of its O_2 if photosynthesis suddenly 'switched off'. If a species evolves with a metabolism that produces a chemical not currently abundant in the atmosphere – C_{new}, a different species that consumes C_{new} needs to emerge quickly before it builds up enough to disrupt the temperature regulation, or the species producing C_{new} must die out, otherwise the whole community is susceptible to extinction.

2 .8 Planets

We define a planet as a system with a particular chemical set and geochemistry. We can therefore run many experiments on a single planet to determine whether a planet has differing end states depending on early conditions.

No external forcing is present on our planets. Each planet's geochemistry remains fixed throughout an experiment and the incoming radiation β_{star} remains constant. Real planets are subjected to changing host star luminosities and changing rates of geological processes over time, however to understand how the biota are able to adapt their host planet, we keep the environment fixed. It is then clearer when emerging phenomena are due to the biota.

An in-depth description of the model can be found in Appendix A.

2 .9 New Features

ExoGaia is based on the Flask model (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010; Nicholson et al., 2017), which features model 'flasks' containing microbe communities. These flasks experience an inflow and outflow of 'nutrients', with the inflow medium at a constant 'temperature'. Microbes change the temperature directly as a byproduct of their metabolism – increasing or decreasing it by a set amount. Differing from previous models such as Daisyworld (Watson and Lovelock, 1983), microbe's do not have localised space, however temperature regulation still

robustly emerges. In the ExoGaia model, instead of microbes directly affecting a temperature, they impact T_{planet} via consuming and excreting atmospheric chemicals. Also differing from the Flask model, the microbes are introduced to an ExoGaia planet, in most cases, before the atmosphere has reached equilibrium.

'Greenhouse World' (Worden, 2010; Worden and Levin, 2011) is a model of microbe communities interacting with insulating chemicals via their metabolism to regulate their environmental temperature. Although similar, ExoGaia has some key differences. Firstly, mutation only takes place in Greenhouse world when the system is in a stable state. Second, Greenhouse systems are seeded with a diverse community of microbes. These communities then reorganise via species dying off until a stable configuration is reached. Greenhouse world therefore demonstrates how diverse communities can scale down to a stable state, whereas in ExoGaia we seed with a single species, and the microbe community must evolve suitable metabolisms to regulate their environment, thus building up a regulating community where Greenhouse world reduces down. All life on Earth shares a common ancestor (Sapp, 2009), and so while it may theoretically be possible for life to form independently multiple times, that does not seem to be the case on Earth, and so we mirror this behaviour in our model.

A slow outflow of chemicals from a planet's atmosphere means that the consequences of microbial actions persist longer than their average lifespan – an important feature not present in previous models – allowing us to see how communities of microbes react to the long-term effects, especially the negative effects, of their metabolism.

3 Method

Using this model, we investigate how the geochemical network of a planet affects the planet's colonisation success and the long-term habitability.

We set the incoming radiation from the 'star' per timestep $\beta_{star} = 500$ and set all microbes to share a preferred temperature $T_{pref} = 1000$. As this T_{pref} corresponds, in our model, to a thermal energy of $\beta_{pref} = 1000$, we see that for a planet to reach habitable conditions, it must have an insulating atmosphere. Recall that all temperatures and energy values in the ExoGaia model are abstract. We generate the insulating / reflective properties of each chemical in our Chemical set by drawing a random number from the range

TABLE 7.1: The greenhouse and albedo properties of chemical set A. The bold chemicals represent the source chemicals. The values in the table represent each chemical's impact on the atmosphere – insulating if positive, and reflective if negative.

Chemical	Greenhouse / albedo properly
1	-0.40
2	-0.47
3	0.40
4	**0.94**
5	**-0.43**
6	0.42
7	0.47
8	0.98
Mean	0.23

$[-1, +1]$. A negative value means a chemical species is reflective, and a positive means it is insulating. We have 8 chemical species in our chemical set. We choose a chemical set such that the average effect of each chemical species is insulating. As $\beta_{star} < \beta_{pref}$, choosing an overall insulating chemical set insures many planets in our experiments will reach habitable planetary temperatures. This allows us to investigate how the microbe community interacts with it's host planet. Choosing an insulating chemical set does bias us to see more potentially habitable planets and thus increase the number of experiments where long-term habitability may be possible, but it does not help microbe communities, once seeded, in regulating their planet. The quantitative values produced by the ExoGaia model cannot be translated into real world values for an abstract model such as this. The qualitative behaviour of the model is the key point of interest. Chemical set A is used for the results presented in this paper, see Table 7.1.

Despite sharing the same chemical set, planets vary hugely from one another due to their geochemical networks. These networks will determine how fast temperatures change, and the value of $T_{abiotic}$, for each planet. As we will see, sharing a chemical set does not result in identical planetary behaviours. The huge number of geochemical network configurations allows for many unique planets. In Appendix B, we present results from experiments with alternative chemical sets, but the same $\beta_{star} = 500$ value, exhibiting the same model behaviours presented with chemical set A, thus showing that chemical set A is not a unique case.

We investigate a range of geological connectivity, C, for our planets: $C = [0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9]$. As our model is abstract, we do not know

what connectivities might be represented in the real world and so we cover almost the full range of possible values excluding $C = 0$, as we certainly live in a world of chemical reactions, and $C = 1$ as not every chemical can react with every other in real world chemistry. By exploring this large range we can investigate the effect connectivity has on the habitability of a planet and see how important this parameter is to the system dynamics.

We perform the following steps for each connectivity in list C:

1. Set up the planet's geological network
   (a) Begin the geological processes on the planet, allowing atmospheric chemicals to build up
   (b) Seed planet with a single species when $T_{planet} = T_{pref}$
   (c) if T_{pref} is never reached, seed after 5×10^4 timesteps
   (d) The experiment ends 5×10^5 timesteps after seeding
2. Repeat step b) 100 times with different random seeds initialising the microbes
3. Repeat steps (a) to (c) 100 times with different random seeds initialising the planet's geological network

There is evidence suggesting that life appeared on Earth as soon as conditions allowed (Nisbet and Sleep, 2001). We treat our simple ExoGaia planets in a similar manner, seeding the planet when $T_{planet} = T_{pref}$ (if this happens at all, some planets will never reach T_{pref}). Because of the way temperature is determined in the model, planet temperatures might never exactly match T_{pref}, so to ensure seeding happens we determine a suitable 'seeding window' $S_w = [T_{pref}, T_{pref} + 50]$. Seeding can occur when planet matches any temperature in S_w but seeding can only occur once. If a seed window has not been passed after 5×10^4 timesteps then an seeding attempt is made once, and the model then continues as usual for 50×10^4 timesteps.

This means that we will often be seeding the planets before the atmosphere is at equilibrium, and the $T_{abiotic}$ of a planet will often be far too hot for our microbe life to survive – effectively undergoing a highly simplified geologically induced greenhouse runaway. We therefore want to investigate whether the model microbes, with their simplified metabolisms, can take control of their host planet once they appear and keep the planet's temperature within habitable bounds.

When we seed our planet with a single species, we seed with a species that consumes chemicals currently available on the planet. Any life with an unviable metabolism would very quickly die out. We could continually seed randomly until a species took hold on the planet, but predetermining that species we are seeding with could potentially survive (it has a food source) saves time.

3 .1 Habitability

There are two types of habitability of interest to us:

- Colonisation success – what percentage of the time a planet is able to support life for $t_{survive} > 10^3$ timesteps.
- Long-term habitability / survivability – what percentage of the time a planet is able to support life for the entire experiment duration: $t_{survive} = 5 \times 10^5$ timesteps.

The colonisation success indicates whether planetary conditions were suitable to support a self sustaining population for some time. 10^3 timesteps is twice as long as the timescale for microbe death; therefore if the biosphere survives longer than 10^3 timesteps, conditions must have allowed microbes to consume enough food to reproduce at a high enough rate to support a stable population. Long-term habitability measures the microbes ability, once they have successfully colonised a planet, to maintain habitable conditions for long time spans.

Over a number of experiments, if a planet has high colonisation success but low late term habitability, it is a planet where life is usually able to colonise the planet and become established, but often fails to survive to the end of the experiment. If a planet has equal colonisation success and long-term habitability, it means that once life is established on a planet, it always survives the full experiment.

4 Results

In a highly abstract model such as ExoGaia, quantitative results cannot be applied directly to real world data, however exploring the qualitative behaviour of the model demonstrates how biosphere-environment coupled systems, such as the Earth and other inhabited planets, might emerge and under

what circumstances. We find that on a diverse array of planets, life is able to 'catch' the planetary atmospheric evolution of it's host planet and maintain habitable conditions. For the majority of ExoGaia planets, the $T_{abiotic}$ of the planet is highly inhospitable, yet we find many model planets hosting biospheres for long time spans. This demonstrates that model biospheres are capable of preventing planetary temperatures from reaching uninhabitable levels, and thus in principle, of regulating planetary temperatures.

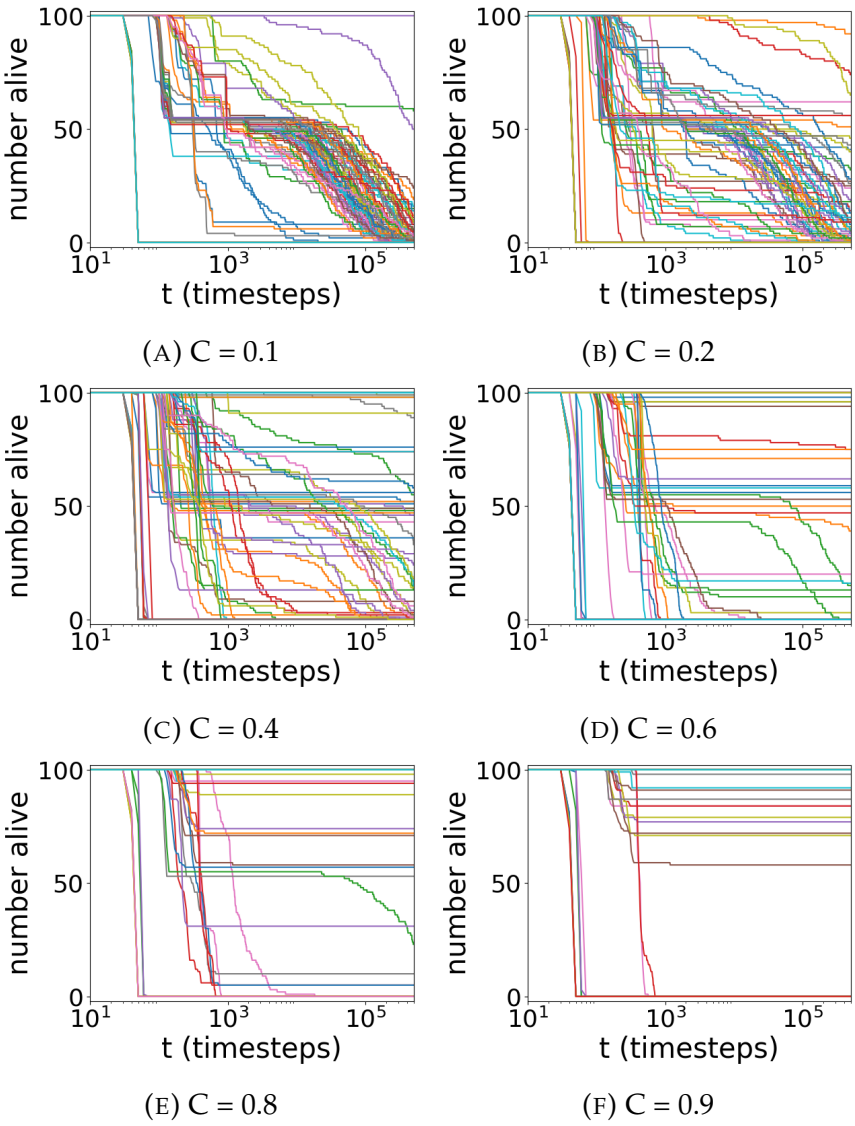
We find that colonisation success and long-term habitability success rates differ between model planets. As we performed 100 experiments on each planet, we can create a survival curve for each planet. Figure 7.3 shows the survival curves – the number of experiments (out of 100) with surviving life – for each planet against time (note the log x-axis).

For low C, Figures 7.3a and 7.3b, there is no strong trend for when systems become extinct. Life is often able to successfully colonise a planet, but the planet is unlikely to experience long-term habitability. For higher C we start to see planets with two distinct experiment outcomes: either life fails to colonise the planet and quickly goes extinct, or life successfully colonises the planet and survives the full experiment. For these planets, the colonisation success and the long-term habitability success of the planet are equal, meaning that if life is able to establish itself, it will survive for an indefinite period of time. This behaviour is explained in Section 4 .3. We see for $C = 0.9$, Figure 7.3f, that all experiments either survive for the full duration, or become extinct early on, with no mid or late time extinctions taking place.

Table 7.2 shows the number of planets that fail colonisation for all 100 experiments, and planets that had long-term habitability for all 100 experiments. In Figure 7.3 the number of planets that always immediately became extinct is difficult to determine, and it is not possible to see the number of planets that always survived the full experiment, so taking Figure 7.3 and Table 7.2 together we get a more complete picture of the different planets' behaviour with changing connectivity.

Based on our results we can determine 5 different classes of planet:

- **Extreme** – Planets that never reach habitable temperatures
- **Doomed** – Planets that do reach habitable temperatures but are unable to support life
- **Critical** – Planets that can be successfully colonised by life, but go extinct at random times



(A) C = 0.1 (B) C = 0.2

(C) C = 0.4 (D) C = 0.6

(E) C = 0.8 (F) C = 0.9

FIGURE 7.3: Each line represents the survival curve of a planet. These survival curves tell us out of 100 experiments, how many are alive for each timestep. Critical planets show extinctions at random times, while Bottleneck planets show an early abrupt dying out and no deaths at longer timescales. Abiding planets have all 100 experiments alive for the whole experiment, and Extreme and Doomed planets always quickly die off early on in the experiment with non surviving to mid or long timescales. The first extinctions seen in each plot show the minimum time it takes for a microbe to starve to death. Note the log x-axis.

- **Bottleneck** – Life either fails to colonise these planets, or successfully colonises and enjoys long-term habitability – a bottleneck effect
- **Abiding** – Life successfully colonises and experiences long-term habitability for all experiments

TABLE 7.2: The number of planets that failed colonisation for 100% of experiments, and the number of planets that had long-term habitability (l.t.h.) success for 100% of experiments. The total number of planets simulated for each C was 100.

C	100% failed colonisation	100% l.t.h success
0.1	18	1
0.2	35	0
0.3	38	7
0.4	36	13
0.5	39	31
0.6	32	42
0.7	15	64
0.8	12	70
0.9	12	77

These planet class definitions are based only on two timescales: the colonisation success timescale which depends on the microbe death timescale; and the experiment length.

We will now explain the regulation mechanism emergent in the ExoGaia model, and then show how a planet's geochemical network affects planetary habitability. We will then present example model planets to demonstrate various model behaviours, and finally show how planetary habitability is affected by connectivity.

4 .1 Regulation Mechanism

The regulation mechanism takes the form of a negative feedback loop. All microbes share the same T_{pref} and the same well-mixed environment, therefore any environmental change impacts all microbe species equally. There is no mechanism by which microbes can evolve only heating or cooling metabolisms, if abundant chemicals of any type are present on a system, microbes can, and will, evolve to consume those chemicals. Therefore it is the collective behaviour of the whole biosphere that leads to regulation rather than any specific microbe species. When $T_{planet} = T_{pref}$, assuming abundant chemicals, microbe populations will increase. The consumption rate of the microbes, K, drops as temperatures diverge from T_{pref}, therefore there are two temperatures where the value of K will lead to a stable population: $T_s^+ > T_{pref}$ and $T_s^- < T_{pref}$. For a stable T_{planet} microbe populations must be stable.

When $\beta_{star} < \beta_{pref}$, where β_{pref} is the thermal energy of a planet at T_{pref}, an insulating atmosphere is required for habitable temperatures. This is the

case for the results presented in the main body of this paper (alternative scenarios are explored in Appendix B). In this scenario, when $T_{planet} < T_{pref}$, the effects of increasing (+) T_{planet} are:

1. + $T_{planet} \rightarrow$ + Population
2. + Population $\rightarrow$ - T_{planet}

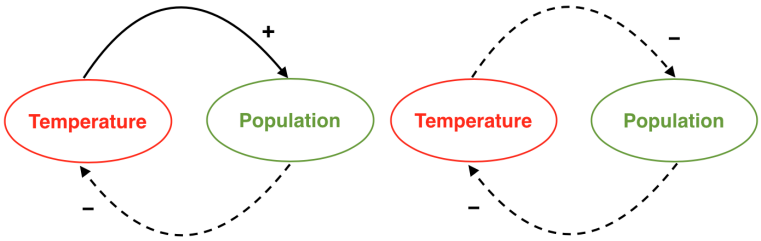
Flipping the signs, we also see that a decrease in T_{planet} leads to an increase in T_{planet}. This forms a negative feedback loop. Increasing T_{planet} improves habitability, which increases K, and thus increases microbe populations. This causes planetary cooling as the insulating power of the atmosphere is reduced via increased microbe consumption. Cooling degrades the environment, reducing microbe populations, and thus causes chemicals to build up in the atmosphere, increasing T_{planet} and bringing us back to the start of the loop. This behaviour is known as 'single rein-control' where the biota collectively form a single 'rein' which 'pulls' the system in one direction, while the abiotic processes on the planet 'pull' the system in the other direction. Rein-control feedback mechanisms have been demonstrated in previous Gaian models, namely in Daisyworld (Wood et al., 2008), and the Flask model (Nicholson et al., 2017).

If instead $T_{planet} > T_{pref}$, the effects of increasing the temperature are now:

1. + $T_{planet} \rightarrow$ - Population
2. - Population $\rightarrow$ + T_{planet}

Now an increase in T_{planet} degrades the environment for life and leads to further rises in T_{planet} in a destabilising positive feedback loop. This results in microbe extinction. Temperature regulation therefore takes place at T_s^- but not at T_s^+. The behaviour seen in both feedback loops is known as feedback on growth (Lenton, 1998).

When $T_{planet} > T_{pref}$ a positive feedback loop in the opposite direction is possible, with runaway planetary cooling occurring until $T_{planet} < T_{pref}$, where the negative feedback loop takes over. However as $T_{abiotic} > T_{pref}$ for a habitable planet, when $T_{planet} > T_{pref}$ a reduction in temperature is unlikely; when habitability is low the abiotic processes on the planet dominate. If T_{planet} rises to above T_{pref}, extinction is the expected outcome. Figure 7.4 shows the positive and negative feedback loops for $T_{planet} < T_{pref}$ and $T_{planet} > T_{pref}$.



(A) Negative feedback loop for $T_{planet} < T_{pref}$ (B) Positive feedback loop for $T_{planet} > T_{pref}$

FIGURE 7.4: The regulating negative feedback loop (a), and the destabilising positive feedback loop (b). Arrows indicate the effect of an increase in the source on the target. The sign indicates whether an increase in the source leads to an increase or decrease the target. In (a) an increase in temperature causes an increase in population, whereas an increase in population causes a decrease in temperature. This forms a negative feedback loop. In (b) an increase in temperature decreases the population, and a decrease in population further increases the temperature. This forms a positive feedback loop.

4 .2 Geochemistry and Habitability

We investigated the underlying geochemical networks for planets of each class to determine what lead to the different planetary behaviours, and found that a planet's geochemical network strongly determines its chance for long-term habitability success. We found two key properties:

- The geochemical network must be such that planetary temperatures recover faster from any microbe induced cooling than the time it would take for the population to go extinct due to starvation.
- For long-term habitability success, the geochemical network must provide many recycling chemical loops.

Different geochemical networks will lead to temperature changes taking place at different rates on different planets. As seen in Section 4 .1, for potentially habitable planets, microbe populations cause planetary cooling. For a planet to be habitable, the geochemical network must be such that T_{planet} increases after microbe induced cooling fast enough to avoid microbe extinction. The rate of temperature change due to abiotic processes alone plays a strong role in determining the colonisation success of a planet.

This is not enough to guarantee long-term habitability however. As seen in Figure 7.3, many planets that were successfully colonised later went extinct. Planets that experienced long-term habitability all shared the feature of

having a geochemical network that provided many chemical recycling loops. For an example, assume that there are only four chemicals in the chemical set and take the geochemical network $1 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 1$, where numbers represent chemical species and arrows are geological processes. In this example, for any microbe metabolism, the geochemistry recycles the waste product back to the food source. This allows a microbe community to 'control' the entire atmosphere with only a single metabolism. By influencing the abundance of one chemical species in the loop, all other chemical species are impacted. Temperature regulation takes place in ExoGaia via the collective actions of the biosphere consuming the atmospherical chemicals without bias, therefore if there are many geochemical recycling networks, and microbes can influence the abundance of many chemical species with fewer metabolisms, achieving planetary regulation is likelier.

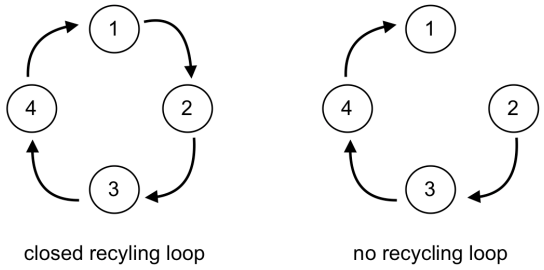


FIGURE 7.5: Circles represent chemical species and arrows represent the geochemical links between them.

Now consider the geochemical network $2 \rightarrow 3 \rightarrow 4 \rightarrow 1$. Chemicals now accumulate as chemical species 1, and the geochemical network does not recycle waste back to food for many metabolisms e.g. $2 \rightarrow 3$ or $3 \rightarrow 1$. These scenarios are depicted in Figure 7.5. Biological links are temperature dependant and change as planetary conditions change. This makes them less stable than the temperature independent geochemical links. Therefore if a geochemical network does not have many recycling loops, and biology must 'complete' many missing links, the system will be more sensitive to temperature changes. Biological links can amplify perturbations throughout the system as T_{planet} impacts the biosphere, which impacts the biochemical network, which further impacts T_{planet}. Therefore these systems are highly susceptible to perturbation, and as any large-scale changes in temperature carry a risk of extinction, these systems are less likely to experience long-term habitability.

4 .3 Example planets

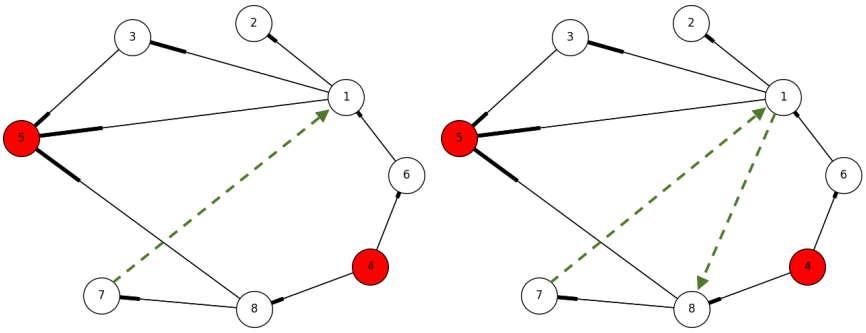
We now present an example planet for each planet class (each example planet has connectivity $C = 0.4$) to demonstrate how the underlying geochemical network impacts a planet's colonisation success and long-term habitability.

Uninhabitable planets

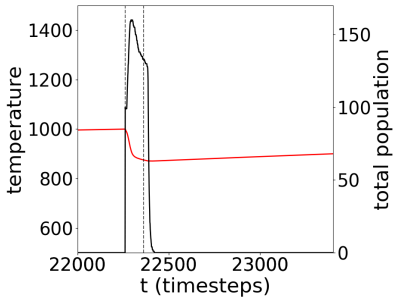
The majority of model planets that fail in every experiment to support life have a $T_{abiotic}$ that's too cold for life to survive. Once seeded, life either cannot metabolise at all, or can only metabolise at levels too low for a stable population, leading to extinction. The underlying geochemistry doesn't have much effect here other than to convert the heating chemical species to cooling ones thus rendering the planet uninhabitable. We will refer to this type of uninhabitable planet as 'Extreme' planets – planets with temperatures that never reach habitable levels.

A small number of uninhabitable planets have a $T_{abiotic}$ such that $T_{abiotic} \geq T_{pref}$. These planets typically have only weakly insulating atmospheres, and temperatures rise very slowly. On these planets when life is seeded, it consumes this insulating atmosphere and causes planetary cooling pushing the planet to uninhabitable temperatures. This in turn causes the microbe population to decline. With a smaller population, the abiotic processes on the planet dominate, however T_{planet} does not rise to the bounds of habitability fast enough and life on the planet goes extinct. We refer to these planets as 'Doomed' planets; although temperatures on these planets do reach habitable levels and microbes can initially metabolise, life always fails to colonise the planet.

Figure 7.6 shows snapshots of the geochemistry and biochemistry of an example Doomed planet that had an $T_{abiotic}$ such that $T_{abiotic} > T_{pref}$. The static geochemistry is represented by black solid lines (with the thick end indicating a positive direction of chemical flow) and the non-static biochemistry is represented by green dashed lines and changes as the microbe community changes. Circles indicate chemical species with source chemicals as red circles. We see the microbe seeding occur when $T_{planet} = T_{pref}$. Microbes are able to establish biochemical links beyond the seed species (Figure 7.6b), however the planet becomes extinct soon after. Figure 7.6c shows that the planet's temperature was increasing very slowly before microbe seeding, and that planetary temperatures do not recover fast enough from microbe



(A) t_{seed} (B) $t_{seed} + 100$



(C) Temperature and total population for early time

FIGURE 7.6: **Example Doomed Planet**: Snapshots of two experiments for the same planet showing the geochemical network in black solid lines, and the biochemical network in green dashed lines. Red circles represent source chemicals. t_{seed} is the time the planet was seeded with life. Plot c) shows temperature (red) and total population (black) against time. C = 0.4. The thick end of the geochemical links indicates positive direction.

induced cooling to avoid microbial extinction. For this planet, the geochemical network was arranged such that abiotic temperature changes happen too slowly to counteract microbial cooling making the planet unsuitable for life. This behaviour, where life reduces the habitability of its environment, is often called 'anti-Gaian' behaviour in contrast to 'Gaian' behaviour where life enhances its environment's habitability.

This behaviour highlights an important feature of the model – a habitable temperature is not enough for habitability. All life interacts with its environment, removing and producing chemicals during metabolisation. As such, life requires an environment where interacting with the environment does not destroy habitability. On these 'Doomed' planets, the atmosphere is only weakly insulating, and atmospheric depletion by the seeded microbes' consumption quickly results in inhospitably cold temperatures. As all life in this model experiences the same environment, it is not possible for microbes to

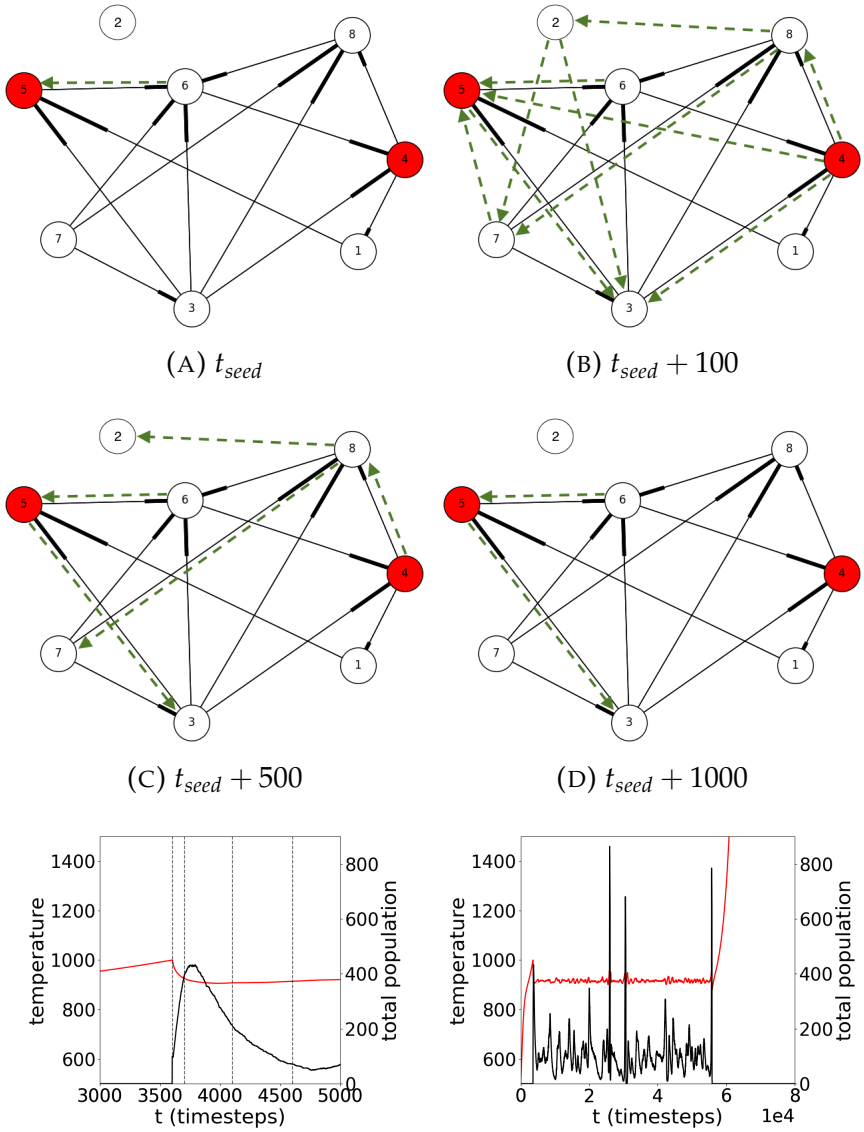
evolve only metabolisms that consume cooling chemicals. If life cannot interact with its environment without pushing it past the bounds of habitability, then despite reaching habitable temperatures, such planets are not good candidates for hosting life. The behaviour of these planets when 'reseeding' – life is reintroduced after going extinct – is included in the experiments is explored in Appendix B.

Critical planets

Critical planets often have high colonisation success however long-term habitability is unlikely. There is no obvious trend in when a Critical planet will become extinct. Critical planets tend to have geochemical networks that cause T_{planet} to rise faster than seen in Doomed planets, meaning that Critical planet temperatures can recover from microbe induced cooling fast enough to prevent extinction. This provides a good environment for colonisation success, however, Critical planet geochemical networks do not provide a large number of chemical recycling networks, therefore certain chemical species can quickly accumulate in abundance and require microbe intervention to prevent large temperature changes.

Figure 7.7 shows snapshots of the geochemistry and biochemistry on a Critical planet, with the temperature and population curves against time. We see that the biochemistry acts erratically; biochemical links quickly infiltrate the geochemical network but later disappear. Figure 7.7e shows a large population spike after seeding which then dies down. Differing from the Doomed planet (Figure 7.6), the temperature recovers fast enough from microbe induced cooling to avoid extinction, and the planetary temperature is then regulated by the microbes for approximately 55,000 timesteps, Figure 7.7f. For Doomed planets, cooling by microbes results in extinction, however for this Critical planet, cooling prevents T_{planet} from rising to inhospitable levels, and thus avoids microbial extinction. In Figure 7.7f we can see the purely abiotic temperature behaviour of this planet when life goes extinct; we see that the planet's temperature immediately and rapidly climbs after microbial extinction. This demonstrates how the same behaviour by life could be classed as 'Gaian' or 'anti-Gaian' depending on the external environment.

Figure 7.7f shows the total population fluctuates around a value of ≈ 120 with extreme population spikes happening a few times – the last of these causing the extinction of the system. These extreme population spikes occur due to the disconnected nature of the geochemical network; chemical species 2 is entirely unconnected to other chemical species geochemically. Figure 7.7c



(A) t_{seed} (B) $t_{seed} + 100$

(C) $t_{seed} + 500$ (D) $t_{seed} + 1000$

(E) Temperature and total population for early time (F) Temperature and total population for the inhabited period of the experiment

FIGURE 7.7: **Example Critical Planet**: Snapshots of a single experiment showing the geochemical network in black solid lines, and the biochemical network in green dashed lines. Red circles represent source chemicals. t_{seed} is the time the planet was seeded with life. Plots e) and f) show temperature (red) and total population (black) against time. C = 0.4. The thick end of the geochemical links indicates positive direction.

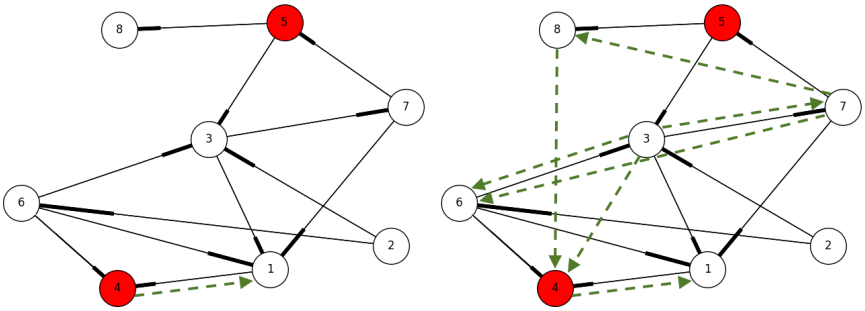
show a biochemical link from 8 $\rightarrow$ 2, however no biochemical link converting chemical species 2 to any other chemical and thus the abundance of chemical species 2 increases rapidly. If a microbe evolves that consumes chemical 2, it will have an abundant source of food. As chemical 2 is a cooling chemical

(see Table 7.2), depleting this chemical species will heat the system, pushing T_{planet} closer to T_{pref} and increasing all microbes' reproduction rates, causing an explosion in population. This population explosion will cause overall depletion of the atmospheric chemicals, and thus, as on average the chemicals in chemical set A are greenhouse chemicals, the temperature will cool and the population will die back down. This scenario is the cause of the first extreme spike seen in Figure 7.7f. Not all Critical planets have completely unconnected chemical species as in Figure 7.7 but they share the common characteristic of a more disconnected geochemical network with fewer purely geochemical recycling loops. Biochemical links are more susceptible to oscillation as changes in one link can have knock on effect to others amplifying the perturbation, thus the more biochemical links required to close recycling loops, the less stable the system is. This is what makes Critical planets susceptible to total extinction.

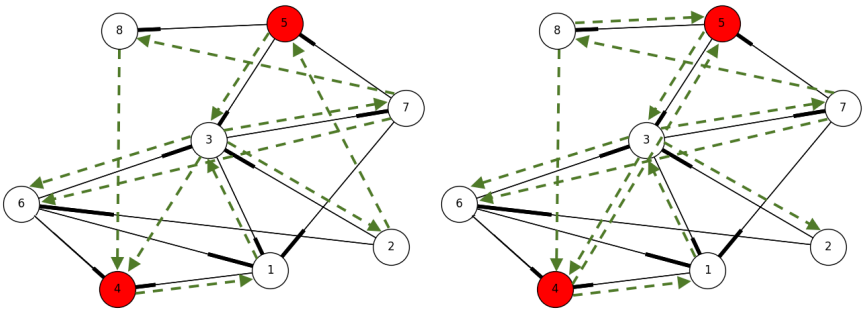
Bottleneck planets

Bottleneck planets either fail to be successfully colonised, or are successfully colonised and life survives the full experiment. Bottleneck planets once successfully colonised are not susceptible to extinction.

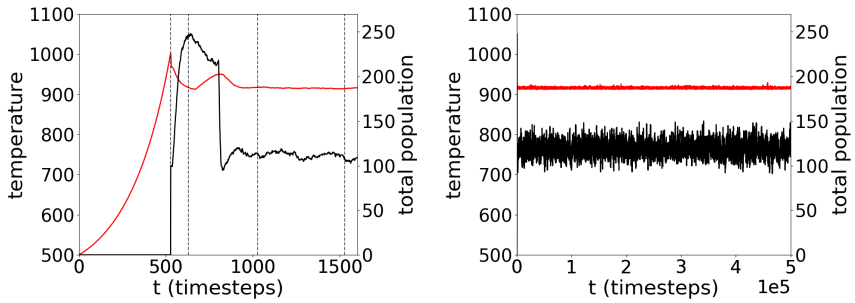
Figure 7.8 shows snapshots of the biochemistry overlaid on the geochemistry for a Bottleneck planet. Examining the geochemistry we see that there are two chemical species, 8 and 4, with no geochemical process converting them to another chemical species. The initial seed species consumes chemical 4. After seeding, there is a population explosion and many new biochemical links are formed including metabolisms consuming 8. The system now has metabolisms controlling both these important chemical species. The population explosion and subsequent consumption of the atmospheric chemicals has caused T_{planet} to cool, causing a sharp decline in the total population, allowing the abiotic processes to take over, warming the planet once more. This improves conditions for life allowing the population to rise again, this time to a more sustainable level, and T_{planet} stabilises under the microbes' regulation. We see that there are many recycling loops already provided by the geochemistry, any waste (barring waste of chemical species 8 or 4) produced by a microbe can be recycled back into its food source, although some loops take more geochemical reactions than others. This makes it easier for the microbes to retain control over their planet's atmosphere as geochemical links, unlike biochemical links, are not prone to temperature dependant fluctuations.



(A) t_{seed} (B) $t_{seed} + 100$



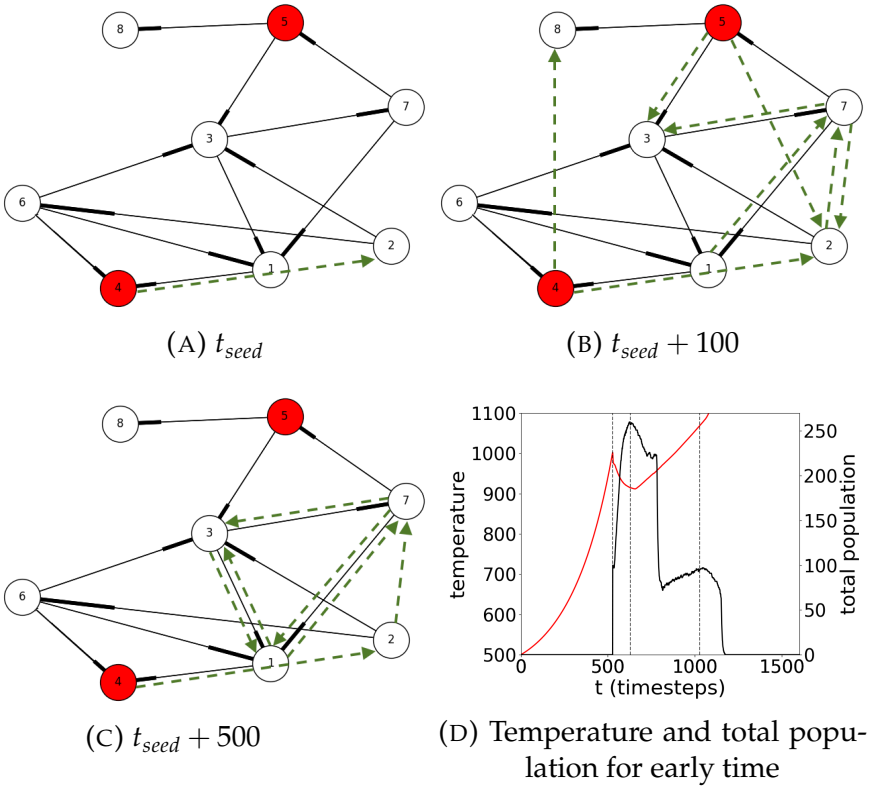
(C) $t_{seed} + 500$ (D) $t_{seed} + 1000$



(E) Temperature and total population for early time (F) Temperature and total population for full experiment

FIGURE 7.8: **Example Bottleneck Planet**: Snapshots of a single experiment showing the geochemical network in black solid lines, and the biochemical network in green dashed lines. Red circles represent source chemicals. t_{seed} is the time the planet was seeded with life. Plots e) and f) show temperature (red) and total population (black) against time. C = 0.4. The thick end of the geochemical links indicates positive direction.

Figure 7.9 shows an experiment for the same planet as in Figure 7.8. This time life failed to survive the bottleneck. We see a very similar pattern as in Figure 7.8 however importantly the microbes in this experiment fail to evolve a metabolism to consume the chemical species 8. The system can survive a



(A) t_{seed} (B) $t_{seed} + 100$

(C) $t_{seed} + 500$ (D) Temperature and total population for early time

FIGURE 7.9: **Example Bottleneck Planet**: Snapshots of a single experiment showing the geochemical network in black solid lines, and the biochemical network in green dashed lines. Red circles represent source chemicals. t_{seed} is the time the planet was seeded with life. Plot c) shows temperature (red) and total population (black) against time. C = 0.4. The thick end of the geochemical links indicates positive direction.

while, compensating for the buildup of chemical 8 by depleting other atmospheric chemicals, however without full control over the atmospheric chemical make-up, the microbes are unable to prevent T_{planet} from rising, and life goes extinct.

Bottleneck planets share the characteristic of having two places where chemicals can accumulate. They otherwise feature many purely geochemical recycling loops. The bottleneck effect occurs early on when life must gain control over the two chemical species with accumulating chemicals; if successful, the recycling loops in the geochemistry prevent the system from fluctuating as wildly as seen in Critical planets. After seeding, Bottleneck planets typically experience a population burst followed by a rapid population decline, before stabilising to a relatively constant total population. The temperature fluctuates the most during this early seeding period. Bottleneck planets can experience population spikes at later times but they are not as

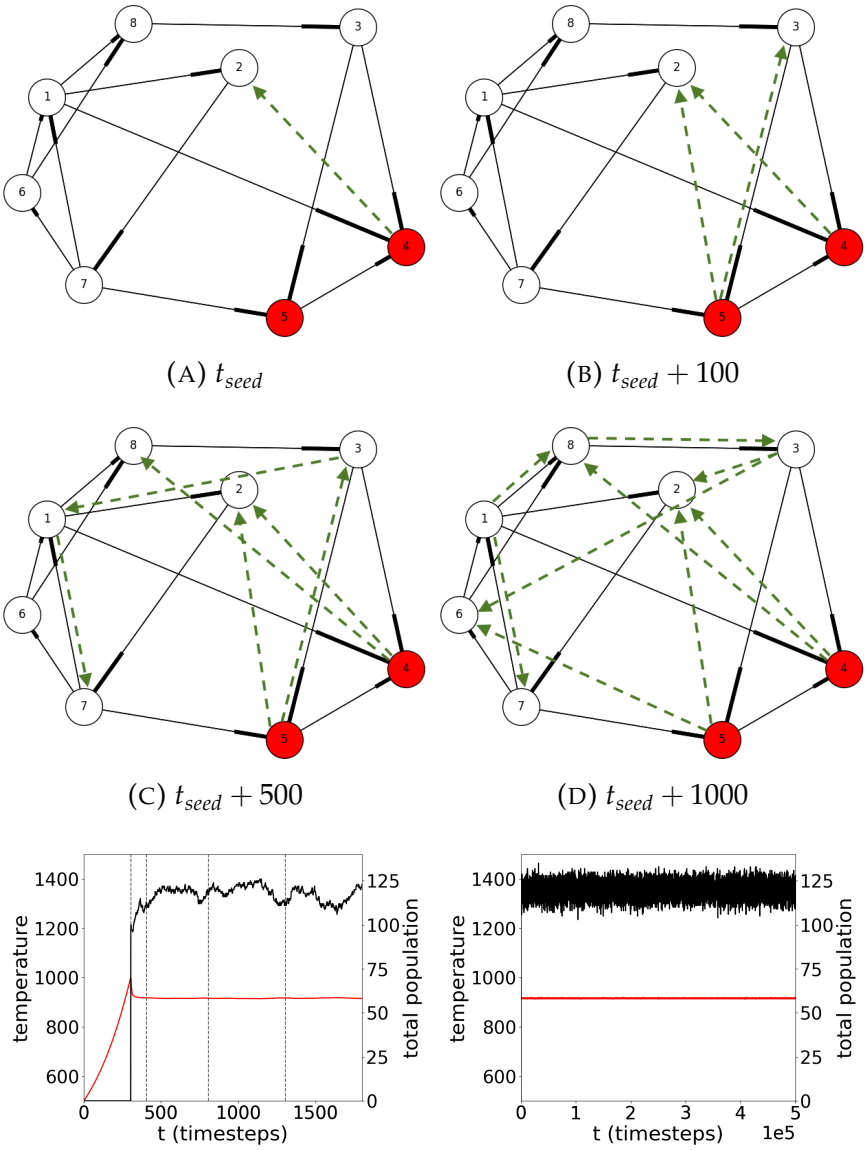
severe as seen for Critical planets (Figure 7.7) and do not carry the same risk of extinction. Bottleneck planets must also have a geochemistry that allows the temperature to rise fast enough following the cooling caused by the early population burst to prevent inevitable extinction, as seen on Doomed planets (Figure 7.6).

Abiding planets

Abiding planets are always successfully colonised by life which then goes on to enjoy long-term habitability for every experiment. Abiding planets provide many purely geochemical recycling loops making the system less prone to perturbation than Critical planets for example, however microbe intervention is still required for continued habitability. One simplification of ExoGaia is that geochemical reactions are temperature independent which prevents abiotic temperature feedback loops. Without the influence of life, the vast majority of Abiding planets will quickly reach inhospitable temperatures during their atmospheric evolution. Therefore, while the presence of many geochemical recycling loop can greatly improve the long-term habitability chances of an inhabited planet, on an uninhabited planet there is no temperature feedback process, and thus nothing to prevent temperatures rising to inhospitable abiotic temperatures.

Figure 7.10 shows snapshots of the biochemistry on an example Abiding planet. The geochemical network of the planet does not provide recycling loops for chemical species 4, but otherwise the geochemistry is well connected with recycling loops present for all possible microbe metabolisms barring those that excrete chemical 4. Figure 7.10a shows the first species seeded on the planet with metabolism $4 \rightarrow 2$. As time progresses, the biochemistry infiltrates more and more of the geochemical network. Figure 7.10e does not show the population explosion and fall back seen for the Bottleneck planet; instead the population rises and reaches a steady value and stays there. Figure 7.10f shows very little fluctuation in the total population or temperature over time.

Abiding planets all share the characteristics of having abundant, purely geochemical, recycling loops. For nearly all microbe metabolisms there are geochemical loops recycling the waste back to food. Abiding planets also typically either have the chemicals well spread between chemical species, or have only a single chemical species that accumulates at high levels. These properties combined make it very easy for life to gain control of its host



(A) t_{seed} (B) $t_{seed} + 100$

(C) $t_{seed} + 500$ (D) $t_{seed} + 1000$

(E) Temperature and total population for early time (F) Temperature and total population for full experiment

FIGURE 7.10: **Example Abiding Planet**: Snapshots of a single experiment showing the geochemical network in black solid lines, and the biochemical network in green dashed lines. Red circles represent source chemicals. t_{seed} is the time the planet was seeded with life. Plots e) and f) show temperature (red) and total population (black) against time. C = 0.4. The thick end of the geochemical links indicates positive direction.

planet's atmosphere and retain that control. With many geochemical recycling loops that are not subject to fluctuation as biochemical links are, the system is highly stable and thus life is able to successfully colonise and enjoy long-term habitability on Abiding planets.

4 .4 Planet Class Frequency by Connectivity

Figure 7.11 shows the frequency of each class of planet against connectivity, C. We see a general trend of Abiding planets dominating at high connectivity, Bottleneck planets present mainly at mid and high connectivity, and Critical planets dominating for low connectivity. The number of Extreme planets increases for mid connectivity and then decreases again. Doomed planets make up a small fraction of the planets for all C.

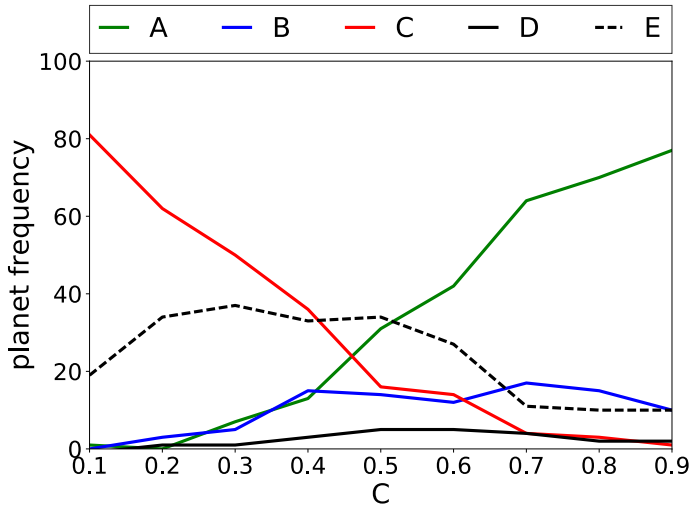


FIGURE 7.11: The frequency of **A**biding, **B**ottleneck, **C**ritical, **D**oomed, and **E**xtreme planets against connectivity for chemical set A

As an abundance of geochemical recycling loops, coupled with biotic temperature feedback loops, leads to higher rates of long-term habitability, it is clear why planets with higher C are more likely to be Abiding planets. With more geochemical links there is a greater chance of geochemical recycling loops. Decreasing C means fewer geochemical links, therefore Bottleneck and Critical planets become more likely with Critical planets dominating for very low C. For low C, biology will have to create more recycling loops itself to successfully regulate the planet's atmosphere, making the system more prone to large scale fluctuations that carry a risk of extinction.

As the source chemicals on average insulate, with few geochemical links most planets for low C will be hot enough for successful colonisation, leading to few Extreme planets. As C increases, the probability of insulating chemicals being converted to reflective chemicals increases and thus so does the frequency of Extreme planets. Increasing C further, the chemicals will become more evenly spread between all chemical species in the chemical set.

TABLE 7.3: The number of planets with habitable $T_{abiotic}$ and number of hot planets for all C

C	N^o habitable $T_{abiotic}$	N^o hot planets
0.1	1	80
0.2	4	62
0.3	3	59
0.4	6	61
0.5	7	59
0.6	13	60
0.7	5	84
0.8	3	87
0.9	2	88

The average abiotic effect of all the chemical species in chemical set A is insulating, and so the frequency of Extreme planets falls. The exact shape of the planet frequency against C curves in Figure 7.11 are an artefact of the chemical set used. However, as they are the result of an abstract model, they cannot correspond to any real world data, and we have only one data point to compare to in any case – Earth. The important feature of ExoGaia is that these planet classes emerge, not the relative frequencies of each. The supplementary data for this paper explores alternative chemical sets to demonstrate that chemical set A is not a special case.

4 .5 Planets with habitable $T_{abiotic}$

A small number of modelled planets have habitable $T_{abiotic}$ values. We can compare how the habitability of these planets compares to those planets with $T_{abiotic}$ values that are too hot for life – 'hot' planets. Hot planets will have passed through T_{pref} in their past allowing for seeding; in order to survive, life will have to take control of its planet's atmosphere to maintain habitable conditions and prevent the temperature from rising to the inhabitable $T_{abiotic}$. Table 7.3 lists the number of planets that have a habitable $T_{abiotic}$ for each connectivity, and compares this number to the number of 'hot' planets. Table 7.3 shows that the habitable $T_{abiotic}$ planets only make up a small percent of the potentially habitable planets.

Comparing to Figure 7.11 we see that the frequency of Critical, Bottleneck, and Abiding planets is far higher than the number of planets with habitable $T_{abiotic}$ values for each C, demonstrating that microbes are frequently successful in colonising planets during a short time period of habitability and then acting to prevent temperatures from rising to inhospitable $T_{abiotic}$ values. For

mid and high connectivities where we see large numbers of Bottleneck and Abiding planets we see that life can not only colonise planets with inhospitable $T_{abiotic}$, but can maintain long-term habitability. This demonstrates that the microbes can be very successful in regulating their planet's atmosphere.

Of the planets with habitable $T_{abiotic}$ values listed in Table 7.3, only one, for $C = 0.4$ was an Abiding planet. None were Bottleneck planets; the majority were found to be Critical and Doomed planets. This shows that planets where $T_{abiotic}$ is habitable are in fact not generally planets that support life long-term. The reason for this is as outlined in Section 4 .3 for the example Doomed planet – life must be able to remove chemicals from the atmosphere to metabolise and survive, and doing so must not push the planet beyond the bounds of habitability. If a planet has a $T_{abiotic} \approx T_{pref}$ then removing chemicals is highly likely to decrease habitability, rather than maintain it (as is the case on many 'hot' planets) thus making such planets, somewhat counterintuitively, mostly poor candidates for long-term habitability.

5 Discussion

The ExoGaia model demonstrates planetary temperature regulation, performed by a simple biosphere. There are two extinction mechanisms in ExoGaia – planetary over cooling caused by microbe activity, or over heating due to abiotic processes following the loss of biotic atmospheric control. Under favourable conditions, life on an ExoGaia planet can enjoy long-term habitability and can prevent temperatures from rising to inhospitable levels as would happen on a planet devoid of life. For colonisation success, microbes require the host planet's temperature to reach a preferred temperature, T_{pref}, during its atmospheric evolution, and require a geochemical network that allows temperatures to recover fast enough after microbe induced cooling to avoid microbe extinction. For long-term habitability, microbes require a planet with a geochemical network that provides many chemical recycling loops. By seeding planets at T_{pref} we have investigated the microbes' ability to maintain the planetary temperature within habitable bounds. The ExoGaia model demonstrates that apparently complex global phenomena such as regulation can arise from the simple interaction of the small parts making up a system. Five distinct planet classes emerge from the ExoGaia model:

- **Extreme** – Planets that never reach habitable temperatures

- **Doomed** – Planets that reach habitable temperatures but are unable to support life.
- **Critical** – Planets that have a higher colonisation success than long-term habitability success.
- **Bottleneck** – Planets that if successfully colonised enjoy long-term habitability.
- **Abiding** – Planets that are always successfully colonised and always have long-term habitability.

We can consider what these results might imply for real planets. Our model predicts that more geologically active planets may be more suitable hosts for life. More geochemical processes provide more potential chemical recycling networks for life to exploit and our model biospheres are more adept at dampening or accelerating pre-exiting geochemical reactions than at forming stable stand alone chemical links. There are clear real world examples however where biological processes are dominant, i.e. the concentration of oxygen in our atmosphere, highlighting the limits of our model for application to the real world.

Which model planet class might Earth belong to? Clearly we do not live on a Doomed or an Extreme planet. We also do not see frequent rapid very large-scale changes in the total population of the biosphere of Earth, perhaps making it unlikely that Earth is a Critical planet. The mass extinctions during the Phanerozoic (Raup and Sepkoski, 1982), were not the regular large-scale stochastic fluctuations typical of our model Critical planets, but rather more akin to regime shifts between periods of quasi-stability. Many of the suspected triggers for these mass extinctions are abiotic phenomena excluded from the ExoGaia model, such as meteor impacts, volcanic events, and changing sea levels (White and Saunders, 2005). These extinctions were also mainly – but not exclusively – of macroscopic organisms, which are a tiny percentage of the biodiversity on Earth even today; from the point of view of microbes, making up the majority of Earth's biomass, these events would probably not be classed as mass extinctions (Nee, 2004). If Venus and Earth are alternate states of the same system (Lenardic, Crowley, and Weller, 2016) perhaps we are on the lucky side of a Gaian bottleneck? We know that certain biological innovations, e.g. the evolution of oxygenic photosynthesis (Hoffman, 2013), and later on the evolution of land plants (Lenton et al., 2012), likely triggered ice ages, the former as oxidation of the atmosphere

mediated collapse of a CH_4 greenhouse effect, and the latter as land plants increased weathering thus increasing the rate of CO_2 removal from the atmosphere. This is perhaps similar to the cooling some Bottleneck planets experience when life is first established. Models of the habitable zone under purely abiotic control, e.g. carbonate-silicate weathering, predict that Earth would be habitable without life (e.g. (Kopparapu et al., 2013)). When examining planets with habitable $T_{abiotic}$ values in Section 4 .5 we saw Critical and one Abiding planet represented. This could suggest that Earth might be an Abiding planet.

Venus' current inhospitable state could indicate it being on the 'losing' side of a Gaian bottleneck as previously speculated, or could indicate a break down of regulation being performed by a hypothetical Venusian biosphere, making Venus a Critical planet. There is no data on how a life-environment coupled Venus system would behave over long time periods, preventing the sort of analysis possible for Earth. If the runaway greenhouse that occurred on Venus was unavoidable, as many models suggest (e.g. (Kopparapu et al., 2013)), then Venus would perhaps most closely correspond to a Doomed planet due to the evidence that it once hosted liquid water (Donahue et al., 1982; Jones and Pickering, 2003) and thus may have once been potentially habitable. Changes in solar luminosity were not considered within the ExoGaia model, and so planets that might have hosted a biosphere, and then lost habitability through unavoidable external factors, do not fit well into the model planet classification system.

We can also consider Mars as observational evidence points to it once having had large bodies of liquid water, e.g. (Milton, 1973). It is not known what the early environment of Mars was like, whether it was warm and wet (Craddock and Howard, 2002), or cold with volcanism and impacts causing transient warm conditions (Wordsworth et al., 2013). If the latter, potential habitats for Martian life might have been heterogenous throughout time and space, possibly preventing any early life from spreading across the planet (Cockell et al., 2012). If this were the case, Mars might most closely correspond to a Doomed planet – a window of habitability existed, however life was unable to flourish. If Mars did at one point host a substantial biosphere, it has clearly lost it. Mars once had a far thicker atmosphere which it has since lost (Pepin, 1994), causing the dry cold conditions on Mars today. Atmospheric loss was not taken into account in the ExoGaia model, however this could perhaps be very loosely compared to an uncontrolled build-up of a cooling chemical on a model planet that a biosphere might mitigate for a

while, potentially making Mars a Critical planet. However, Critical planets are theoretically habitable indefinitely, while any planet undergoing significant atmospheric loss will experience drastic changes in its surface environment, making this comparison far from ideal. There is ongoing speculation that life might yet be found on Mars in sparse pockets (Wilkinson, 2006). ExoGaia is mainly concerned with large-scale planetary regulation, and therefore small refuges of life with little to no impact on global parameters are predicted to impact model results only if conditions improved to allow this life another chance of becoming globally established (see Appendix B for experiments along this theme).

With a highly simplified and abstract model like ExoGaia, no strong predictions can be made for individual planets, and comparisons between real planets and model planet classifications highlight the many limitations of the model. More complex future versions of ExoGaia could begin to address some of the questions raised by considering specific planets within the ExoGaia framework and future space missions to Venus and Mars might provide more data to compare with model planet classifications. It is difficult to determine which class a planet might fall into based on a single time point; the planet classes in ExoGaia are best identified by looking at the whole planet history. Therefore, any methods that can provide long timescale observations of planets would provide the best data for comparison with model predictions.

The ExoGaia model adds to the narrative that for a planet to remain habitable, it must be inhabited (Lenardic, Crowley, and Weller, 2016). It suggests that geologically active planets still early in their atmospheric evolution would be the most suitable candidates for colonisation by life and agrees with the idea that when searching for inhabited exoplanets we should look for planets with atmospheres in disequilibrium (Lovelock, 1965). Our model suggests that many planets that have had life will have lost it, however that some, with the right geological conditions, can enjoy long-term uninterrupted habitability. Currently with only one data point – the Earth, we cannot draw any conclusions. As more exoplanets are found, their macro properties determined, and their atmospheres analysed, we will have more data available to compare with model predictions.

Further work should explore how the ExoGaia model behaviour is impacted by adding temperature dependant abiotic processes, and the effects of changes in solar luminosity or other abiotic perturbations. Our model

microbes could also be made more complex, as microbes can be found in almost any part of our globe, from the Mars-like conditions of the Antarctic dry valleys (Siebert et al., 1996) to hydrothermal vents at around 122^{o}C (Clarke, 2014), a fact not reflected in our model where microbes have a universal temperature preference. Adding spatial structure to models has been shown to be very important in work in theoretical ecology over recent decades (Nee, 2007) and therefore is an obvious next step in developing this model. Introducing spatial heterogeneity into the model would also allow life to seek refuges during periods of extreme climate change, similar to how life is thought to have survived in small oases during the snowball earth events, or speculated to possibly persist on Mars today. The change in model dynamics in response to adding spatial structure would be an important next step in improving the applicability of the ExoGaia to real planets.

A ExoGaia Model Description

Code made available upon reasonable request to corresponding author.

The ExoGaia model uses agent based dynamics to describe a biosphere consisting of simple microbes interacting with a host planet via consumption and excretion of atmospheric chemicals. These chemicals determine the surface temperature of the planet. In this appendix each part of the model will be described in detail and then the experiment method will be presented at the end.

A .1 Microbes

The microbes consume chemicals as food and excrete chemicals as waste products. A particular microbe's food and waste product are encoded in the genome of each microbe species. All microbes share the same ideal temperature (i.e. the temperature which results in the maximum growth rate). Microbes grow by consuming chemicals and converting them to biomass. They reproduce asexually by splitting once their biomass reaches a threshold. Biomass is decreased by a fixed amount per timestep to represent the cost of staying alive. Microbes die if their biomass drops below a fixed threshold, which can happen due to food limitation or temperature limitation leaving the microbes unable to consume the chemicals present.

In the code we do not record microbes of the same species individually as doing so would slow the simulations considerably. Instead we group microbes of the same species together and record the species' total biomass. Thus each species can be thought of as a list M:

$$M = (g, N, B, F, W, T_{pref}) \tag{7.4}$$

where g is the species' genome (represented as a decimal number), N is the population of the species, B is the total biomass of the species, F is total number of consumed food chemicals not yet converted into biomass, W is the total number of waste chemicals not yet excreted by members of the species, and T_{pref} is the temperature that maximises the growth rate for species M. All species share the same T_{pref}.

Genotype

The genotype of a microbe is recorded as the decimal representation of an 8 bit binary string, and this is used to group microbes into species. Microbes

TABLE 7.4: Example microbe metabolism look up table

Index	Food Chemical	Waste Chemical
0	2	6
1	4	1
2	1	2

that share the same genome are of the same species. We create tables for microbe chemical consumption and excretion rules, and this genome is used as the reference to look up the particular metabolism for a microbe. These tables are generated in the following way: for each possible genome, a chemical species is selected at random to be the food source for microbes of that genome. Another chemical species is then selected at random to be the waste for microbes of that genome. The food source and waste of a microbe must not be the same, so if the waste chemical species selected is the same as the food, another chemical species is chosen at random until these are not the same. All microbes consume only one type of chemical and excrete only one type of chemical. The index of a microbe's metabolism in the table is the decimal value of the microbe's genome. With an 8 bit long binary genome there are 256 possible species (as each gene in a genome can have the value 0 or 1).

Table 7.4 shows an example look up table. To use Table 7.4, for a microbe with genome 000000010, we convert to its decimal value, 2, and find that this microbe has metabolism $1 \rightarrow 2$ i.e. it consumes chemical species 1 and excretes chemical species 2.

Chemical Consumption

When a microbe is selected to consume, it will attempt to eat K_j units of its chemical food source (the value of K_j depends on how closely the planetary temperature matches the microbes' preferred temperature, and the microbes' sensitivity to the environment), and will be successful if the chemicals are available.

For simplicity we limit our microbes to single chemical metabolisms, meaning that a microbe only consumes one type of chemical, and only excretes one type of chemical, with the limitation that no microbe may consume what it excretes.

Metabolism

The microbes convert their food into biomass in an inefficient process that produces waste product. The efficiency of this conversion is given by θ, and

the amount of biomass produced is given by:

$$B_j = \theta F_j \tag{7.5}$$

where B_j is the number of biomass units produced and F_j is the number of food units currently 'contained' with a microbe j. The waste excreted in this process is given by:

$$W_j = (1 - \theta) F_j \tag{7.6}$$

where W_j is the number of waste units produced, which are released into the environment after the biomass has been created, in the form of the chemicals determined by microbe j's specific metabolism (e.g. see the look up table example in the previous section).

Effect of temperature on metabolic rate

The state of the abiotic environment affects the rate at which microbes can consume chemicals which in turn affects the rate of biomass production and thus the growth of the microbes. A microbe will attempt to consume an amount of chemicals K_j each timestep with the demand being met depending on chemical availability. K_j is calculated for each microbe j as a function of the difference between the microbes' ideal temperature and the current planetary temperature. This function is has a Gaussian form and falls away smoothly from its maximum as the distance between the optimum and the current environment increases. This is a widely used assumption when modelling an organism's response to the temperate of its environment. Mathematically we write this as:

$$K_j = \psi_j K^{max} \tag{7.7}$$

$$\psi_j = e^{-(\tau p_j)^2} \tag{7.8}$$

$$p_j = \sqrt{(T_{planet} - T_{pref})^2} \tag{7.9}$$

where K^{max} is a constant determining the maximum rate of consumption for any microbe, ψ_j is a microbe specific measure of the microbe's satisfaction with the current abiotic environment, τ is a universal constant parameter that determines how sensitive the microbes are to their environment ($\tau = 0$

means the microbes are not affected by the abiotic environment at all, and a higher τ means the microbes become more sensitive to the abiotic conditions). The effects of changing this τ parameter has on system dynamics has been explored in the Flask model (e.g. (Nicholson et al., 2017)) on which this model is heavily based on. p_j is a measure of the (positive) distance between the current environmental temperature, T_{planet}, and the microbe's preferred temperature, T_{pref}.

Maintenance Cost

There is a fixed biomass cost λ of staying alive for each microbe. This reduces a microbe's biomass by a constant rate. This cost represents the energy costs of maintaining cellular machinery and metabolic inefficiency. This cost is assumed to be lost as unrecoverable heat radiation. This ensures that the chemicals cannot be infinitely recycled and it sets the carrying capacity of the system. This carry capacity is reached when the total heat dissipation matches the energy supplied in the form of chemicals, i.e. the food the microbes consume. As any heat dissipation of the microbes in the real world due to metabolic inefficiency is many orders of magnitude smaller than the effects of the atmospheric composition on planetary temperatures, we neglect this heat dissipation when calculating planetary temperatures.

Reproduction and Mutation

If the microbe is able to consume enough chemicals to reach the reproduction threshold T_R, it will reproduce asexually, splitting in half. Half of the biomass with go to the new microbe and the parent microbe will be left with half its biomass. The new microbe will have the same genome as the parent unless a mutation occurred during the reproduction. There is a small constant probability of mutation, P_{mut}, for each locus. During a reproduction event, the code iterates through the genome of the new microbe and if a mutation occurs at a locus then the gene at that point will be 'flipped', turning it to 0 if it were previously 1, or to 1 if it were previously 0. This new mutant genome will then dictate the new microbe's metabolism.

Death

If a microbe's biomass falls to a starvation threshold T_D the microbe will starve to death. There is another small probability of death P_D that represents death by hazardous mutation or damaging local environmental changes etc.

When a microbe dies its biomass is removed from the system, as if the dead microbe, for example, fell to the bottom of the ocean. During a death event, we first check to see if the selected microbe has enough biomass to avoid death by starvation. If the microbe has not starved to death it will be killed with probability P_D.

A .2 Selecting a microbe

We use agent based dynamics in our model. This means within a timestep, a microbe is chosen randomly for an event and time is effectively frozen while the microbe performs that event. Time is then restarted and another microbe is chosen at random for an event.

As we record microbes grouped together in a species (Equation 7.4), for any particular species we have the population of the species, the total species biomass, and the total consumed food not yet converted into biomass. To select a single individual of a particular species we therefore need to determine how much biomass and unconverted food this individual has. If a microbe is selected for a reproduction event, we need to know how much biomass it has to know if it has reached the reproduction threshold for example.

There will be variation between individuals of a species and so we assume a normal distribution of biomass and unconverted food between individuals of a species. The biomass normal distribution is centred around the average amount of biomass B_{av} per microbe (i.e. the total species biomass divided by the species population), with standard deviation of the distribution is $B_{av} \times 0.1$. The normal distribution for the unconverted food is the same but with F_{av}, the average amount of unconverted food per microbe, instead. The standard deviation for both distributions is small, resulting in a small level of variation in the population. Therefore most individuals of the same species will have the same biomass and food levels.

Once we have selected a microbe and calculated its biomass and food level, the microbe can then attempt to perform the event it was selected for.

A .3 Planet setup

Each planet has a well mixed atmosphere with no spatial element. The atmosphere is characterised by chemicals. There are 8 possible chemicals in ExoGaia, although not all chemicals have to be present in the atmosphere at the same time. The chemicals present in the atmosphere may be consumed

by microbes and converted into biomass, and the atmospheric chemical composition determines the temperature of a planet.

'Temperature' in ExoGaia

When calculating temperatures in the ExoGaia model we make a simplification of the Stefan-Boltzmann law. Instead of $\beta \propto T^4$, where β is the incoming energy to the planet from the 'star' and T is planetary temperature, we simplify to $\beta \propto T$. This approximation has been used before in Daisyworld to make determining the underlying regulation mechanisms easier. It has been noted (Watson and Lovelock, 1983; Saunders, 1994; De Gregorio, Pielke, and Dalu, 1992; Weber, 2001; Wood, Ackland, and Lenton, 2006; Wood et al., 2008) that this simplification does not greatly change the overall behaviour of the Daisyworld model. The Stefan-Boltzmann equation is close to linear at real world habitable temperatures, i.e. near 22^oC. In ExoGaia, we are only interested in planetary dynamics when there is life on a planet, so while the 'temperature' in the ExoGaia model is not constrained, we are only interested in a narrow range of temperatures where life is possible. The temperature behaviour outside this range is not important to the model results. We use an unrealistic T_{pref} for our model microbes to highlight the abstract nature of the model, however as a near linear relationship exists at habitable conditions on Earth, and we are striving to simplify the model abiotic environment as much as possible, we take $\beta \propto T$, where β is the energy provided to the planet by the host star per timestep, T is temperature. We then make a further simplification and take the value of β to be equal to the value of T.

Chemical Species

In ExoGaia we have different 'chemical species' as an abstract representation of real-world atmospheric gases e.g. CO_2, CH_4, or O_2. These abstract chemical species are not meant to mimic any specific real world chemistry. Each chemical species insulates or reflects by a particular amount. The maximum reflective or insulating property of a chemical species i is represented by a_i. These a_i values are taken from the range [-1, +1]. A negative a_i corresponds to a reflective chemical species, and a positive a_i means it is insulating. A positive a_i might represent for example the maximum insulating effect of an atmosphere saturated with CO_2. The strength of the effect exhibited by any chemical species, S_i, depends on the number of particles of that chemical in the system, e.g. the abundance of CH_4 say in the atmosphere:

$$S_i = a_i \tanh\left(\frac{n_i}{D}\right) \tag{7.10}$$

where n_i is the abundance of chemical species i, i.e. the number of particles of chemical i present in the atmosphere, and D is a large number to make the effects of a single 'particle' of each chemical species small. This enables large populations to be supported where the individual effect of a single microbe's consumption and excretion of chemicals is small. We use the hyperbolic tangent as it is a function that smoothly varies between 0 and 1. The maximum effect any chemical species, i, can have is determined by its a_i value and by using the hyperbolic tangent we can cap the reflective or insulating effects of a chemical species to its a_i value. This does not prevent runaway temperature changes in the model, as seen when planetary temperatures rise to above the microbe's ideal temperature.

A subset of chemical species are chosen as 'source chemicals'. These are chemical species with an inflow from what we could think of as the 'mantle' of the planet, e.g. CO_2 from volcanoes. Each source chemical has a constant inflow rate I_N, and there are N_S source chemicals. This inflow is kept at a constant rate per timestep for the full experiment. Any chemical species that is not a source chemical does not exist in the atmosphere unless it is produced by a geochemical or biochemical process.

Atmospheric properties and planetary temperatures

The state of the atmosphere is given by a vector V:

$$V = (n_1, ..., n_N) \tag{7.11}$$

where n_i is the abundance of chemical species i, and N is the number of chemical species. As each chemical species in the model has an insulating or a reflective property, the planet atmosphere's insulating or reflective effect will depend on the chemical composition of the atmosphere.

We define A_I as the fraction of the planet's current thermal energy retained by the atmosphere via insulation, and A_R as the fraction of incoming solar radiation reflected by the atmosphere. The total reflective and insulating properties of the atmosphere depends on the amount of each type of chemical present. We calculate A_R, and A_I in the following way:

$$A_R = \sum_{i \in R} -a_i \tanh\left(\frac{n_i}{D}\right) \tag{7.12}$$

$$A_I = \sum_{i \in I} a_i \tanh\left(\frac{n_i}{D}\right) \tag{7.13}$$

R is the set reflective chemical species and I is the set of insulating chemical species. n_i and D are the same as for Equation 7.10. A_R and A_I are constrained to be between 0 and 1, as the maximum amount of thermal energy a planet can retain is the energy it currently has, and the maximum amount of incoming radiation that can be reflected is the amount incoming from the host star, so we also have:

$$\text{if } A_R > 1 \rightarrow A_R = 1 \tag{7.14}$$

$$\text{if } A_I > 1 \rightarrow A_I = 1 \tag{7.15}$$

We define β_{planet} as the planetary thermal energy and β_{star} as the incoming solar radiation per timestep. We then calculate β_{update}, the updated thermal energy of the planet including the insulating effect of the atmosphere in the following way:

$$\beta_{update} = A_I \beta_{planet} + (1 - A_R)\beta_{star} \tag{7.16}$$

Using the simplification in Section A .3, the β values correspond to temperature values, so that if the thermal energy of a planet was β_{planet}, then the value of β_{planet} will be the same as the value of T_{planet} – the temperature of the planet.

Chemical inflow and outflow

There is a constant rate of inflow of source chemicals. Each timestep, I_N particles of each source chemical will be added to the system. There is a rate of outflow from every chemical species that is abundance dependant. Each timestep every chemical species will experience an outflow of $n_i \times O_N$ where n_i is the abundance of chemical species i, and O_N is a constant rate of outflow. Therefore more abundant chemical species will experience a higher rate of outflow than less abundant ones.

Geochemistry setup

Each planet has geochemical reactions taking place throughout the experiment. For our geochemistry, we have links between chemical species converting one chemical type to another. The process is assumed to be 100% efficient, so one particle of chemical A would be converted to one particle of chemical B. Links between chemical species can only flow in one direction, so if we have a process converting chemical $A \rightarrow B$, we cannot then have another geochemical process converting $B \rightarrow A$. Other routes are allowed though, i.e. $B \rightarrow C \rightarrow A$ for example. This simplification makes it simpler to track chemicals as they move through the system. Real world systems have chemical reactions that can be reversed, however we could also consider this simplification to be the net movement of chemicals once each direction of the reaction has been taken into account. If $A \rightarrow B$ and $B \rightarrow A$, we can still describe the overall movement of chemicals between A and B with a link of either $A \rightarrow B$ or $B \rightarrow A$.

Geochemical reactions take place at a rate that depends on the abundance of the reactant chemical species. Each geochemical link is randomly assigned a value taken from the uniform range $[0, 1)$ which we call the 'link strength'. This number determines what percentage of the reactant chemical species is converted to the product chemical species due to the geological process, per timestep. E.g. if we have a geological link: $A \rightarrow B$, with strength 0.2, this means every timestep 20% of chemicals type A are converted into chemicals of type B.

If we have a matrix G that represents a planet's geochemical reactions, G_{ij} would be the flow from chemical species i, to chemical species j due to a geochemical reaction. If $G_{ij} > 0$, then $G_{ji} = 0$ as we don't allow for links flowing between the same two chemical species in opposites directions. For a particular connectivity, say $C = 0.1$, each chemical species has 10% chance of being connected to another. We then determine the strength of the connection, i.e. how fast the process is that converts A to B. We set up our geochemical processes in the following way.

To populate the geochemical reaction matrix G, we consider each pair of chemical species in turn. The connectivity C tells us the probability that these two chemical species will be connected by a geological reaction, or link. We generate a random number r_1 taken from the uniform range $[0, 1)$, and if $r_1 < C$ then our chemical species are connected by a link. If $r_1 \geq C$ the two chemical species are not connected.

If the chemical species are connected we then generate another random number, r_2, also from the uniform range $[0, 1)$ to determine which direction the link flows in, e.g. $A \rightarrow B$ or $B \rightarrow A$ with each direction having equal probability.

Once the direction of the link is determined, the strength of the link is then found by generating a third random number, r_3, (from the uniform range $[0, 1)$) and the link strength $L_s = r_3$. We repeat this process for each pair of chemical species.

Thus we end up with a matrix G of the following form:

$$G = \begin{bmatrix} 0 & 0 & a_{2,0} & 0 & 0 \\ a_{0,1} & 0 & 0 & a_{3,1} & 0 \\ 0 & a_{1,2} & 0 & a_{3,2} & 0 \\ 0 & 0 & 0 & 0 & a_{4,3} \\ 0 & a_{1,4} & 0 & 0 & 0 \end{bmatrix} \tag{7.17}$$

G contains all the geological processes happening on a planet, with their strength and direction. All the G_{ii} indices are 0, and where $G_{ij} > 0$ it is always true that $G_{ji} = 0$. If $G_{1,2} = 0.7$ for example, it means that every timestep 70% of chemical species 1, will be converted into chemical species 2.

Each timestep we can therefore loop though G to determine where chemicals are moving due to geochemical processes. For a non zero G_{ij} value, chemical species i will be depleted by $n_i G_{ij}$ and chemical species j will be incremented by the same amount due to the geological process. We do this for each geochemical process and add up the total amount of chemicals added to or removed from each chemical species for each timestep.

A .4 Seeding a planet

A planet is seeded with microbial life when the temperature of the planet T_{planet} equals the microbes' preferred temperature T_{pref}. Because of the way temperature is determined in the model, planet temperatures might never exactly match T_{pref}, so to ensure that seeding still occurs we determine a suitable 'seeding window' S_w – a small temperature range close to T_{pref}. Seeding can occur when planet matches any temperature in S_w but seeding only occurs once. These T_{pref} and T_{planet} temperatures correspond to thermal energies, and using the simplification in Section A .3 we can take the values of T_{pref} and T_{planet} to be same as the values of the corresponding thermal energies β_{pref} and β_{planet}.

For the case where $\beta_{star} < \beta_{pref}$ we require an insulating atmosphere for habitability. Therefore we determine our seed window, S_w, as the range $[T_{pref}, T_{pref} + 50]$. As we know for $\beta_{star} < \beta_{pref}$ we must have an insulating atmosphere for potential habitability, the S_w range goes higher than the ideal temperatures, so that if temperatures never exactly match T_{pref} as the temperatures continue to rise, seeding still takes place, and life will still be seeded at a hospitable temperature.

For the case where $\beta_{star} > \beta_{pref}$, we need a cooling atmosphere for habitability therefore we set $S_w = [T_{pref} - 50, T_{pref}]$. The logic is the same, however here, as the atmosphere on a potentially habitable planet in this setup will be a cooling atmosphere, the temperature will be falling when it passes through T_{pref} so we allow for slightly cooler temperatures in case $\beta_{planet} = \beta_{pref}$ in the simulation never takes place exactly.

When $\beta_{star} = \beta_{pref}$, we have an extra requirement that is automatically fulfilled in the previous two scenarios. When we seed with life, we require there to be food for the life to consume. When β_{star} is far from β_{pref}, we know that when the planet's temperature becomes habitable, it is because an atmosphere has built up. When $\beta_{star} = \beta_{pref}$, seeding could occur when no food was present. To deal with this we add an extra requirement for seeding when $\beta_{star} = \beta_{pref}$. S_w is now in the range $[T_{pref} - 50, T_{pref} + 50]$ as a potentially habitable planet could have either a cooling or insulating atmosphere, and now we require that at least one chemical species in the system must have an abundance greater than 1000. This means that although conditions will start with $T_{planet} = T_{pref}$ seeding is delayed until there are some atmospheric chemicals present for the microbes to consume. These chemicals will likely alter planetary temperatures and thus degrade the environment, however provided an abundant food becomes available before the seed window is missed, seeding will take place.

For all scenarios, when seeding a planet, we seed with one species and we seed with M_N individuals of that species. We choose the seed species at random, however we ensure that the species chosen has an abundant food source available to it. If species A consumes chemical C_A, if there are greater than 1000 units of chemical C_A in the atmosphere at the time of seeding, species A is a suitable seed species. If there are fewer than 1000 units of C_A present in the atmosphere at the time of seeding then species A is not a suitable seed species and another species is chosen at random until a suitable species, that consumes a presently abundant chemical, is found. This makes biological sense as a species will not evolve to consume a nonexistent food

source.

If a seed window has not been passed after 5×10^4 timesteps then an seeding attempt is made once, and the model then continues as usual for 50×10^4 timesteps.

It seems sensible that life on Earth will have emerged to initially consume something plentiful which is why we take this approach in our model. If life initially emerged to consume something not plentiful then extinction will have quickly followed. As life did indeed emerge on Earth, either it initially had a stable food source, or it emerged many times and went extinct until a life-form that consumed a food source abundantly present emerged and avoided extinction via starvation.

A .5 Model Timesteps

We use agent based dynamics to run the simulation and a timestep is broken down into 'iterations'. The number of iterations per timestep depends on the the number of microbes alive in the system at the start of the timestep. In reality, microbes eat food, create biomass, excrete waste, reproduce, and die all in parallel with one another. The model steps performed within a timestep in the ExoGaia model would also ideally all be computed in parallel but computational limitations prevent this, and so for agent based dynamics we effectively freeze the system while a selected microbe performs an action. Therefore timesteps are broken down into iterations. An iteration consists of the following steps:

- A microbe is randomly selected for a chemical consumption event
- A microbe is randomly selected for a biomass creation event
- A microbe is randomly selected for a reproduction event
- A microbe is randomly selected for a death event

These events are repeated N_M times each where N_M is the microbe population at the start of a timestep. A microbe selected for an event will not necessarily perform that event. For example, the microbe might not have enough biomass to reproduce, or the temperature might be too hot or cold for a microbe to consume chemicals. Being selected for an event means that a microbe will perform that event only if conditions allow, and depends on the probability of the event successfully occurring.

We also break down the inflow and outflow of chemicals and to prevent sudden changes at the the start of each timestep. If we simply added and deducted the chemical flow amounts at the start of each timestep, microbes selected at the beginning of a timestep could see a very different world to those selected at the end of a timestep and large sudden changes could occur between timesteps. Although these effects would largely average out due to the random selection of microbes during each timestep, a single large influx per timestep could be thought of as a periodic perturbation on the system which could affect the results seen. To counter this, we calculate the total inflow (from external sources if a source chemical, and from inflows due to geological processes) and outflow of each chemical species at the start of each timestep and divide this by the number of iterations in the timestep, i.e. the microbe population at the start of the timestep, N_M:

$$N_i^{change} = I_N - O_N N_i^{ab} / N_M \tag{7.18}$$

I_N is the number of units of chemical inflow per timestep, O_N is the percentage outflow, and N_i^{change} is amount we increment chemical species i's abundance each iteration. This results in the same quantity of chemicals being added / removed from the system as if there was just one update at the start of the timestep, but it results in a much smoother transition and means that microbes selected at the start and end of a timestep will see much more similar worlds. Of the life events of a microbe, only chemical consumption depends on the external environment which means only one event within an iteration is dependant on environmental conditions. The other events: biomass production, reproduction, and death, depend only on internal parameters of a microbe (amount of biomass etc.) and P_D which is not affected by environmental conditions. Therefore it is not necessary break chemical inflow / outflow further down to increment between each iteration step.

In this process, we treat chemical levels as continuous but the microbes always treat the chemicals as units. So for a timestep, each iteration we might add 10.7 chemical units per iteration, but microbes in the system can only act on the integer amounts of chemicals present.

A .6 Method

We perform the following steps for each connectivity in list C:

1. Set up the planet's geological network

TABLE 7.5: Planet parameters

Parameter	Value	Description
N	8	Number of chemical species
N_S	2	Number of source chemistry
I_N	75	Rate of chemical influx (units / timestep) per source chemical
O_N	0.0001	Rate of chemical outflux (percentage / timestep)
$P_{abiotic}$	1	Probability of a chemical species having an insulating or reflecting effect
a_i	[-1, +1]	A chemical species's reflective (if -ve) or insulating (if +ve) effect on the planet generated from range [-1, +1]
β_{star}	[500, 1000, 1500]	Solar radiation provided by host star / timestep
D	75,000	A constant to dampen the effects of a single 'particle' in the atmosphere
C	[0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9]	Planet connectivity, i.e. the proportion of chemical species connected by geochemical processes

   (a) Begin the geological processes on the planet, allowing chemicals to build up

   (b) Seed planet with a single species when $T_{planet} = T_{pref}$

   (c) if T_{pref} is never reached, seed after 5×10^4

   (d) The experiment ends after 5×10^5 timesteps after seeding

2. Repeat step b) 100 times with different random seeds initialising the microbes

3. Repeat steps (a) to (c) 100 times with different random seeds initialising the planet's geological network

A .7 Parameters

Tables 7.5, 7.6, and 7.7 show the parameter values used to generate the data presented in this paper.

TABLE 7.6: Microbe parameters

Parameter	Value	Description
B_R	120	Reproduction threshold (biomass units)
B_D	50	Starvation threshold (biomass units)
P_{mut}	0.01	Probability of mutation at each locus during reproduction
P_D	0.002	Probability of death by natural causes (other than starvation) at each timestep
K^{max}	10	The maximum number of chemicals a microbe can eat per timestep when conditions are ideal
N_{gene}	8	Microbe genome length
λ	1	Maintenance cost (biomass units / timestep)
θ	0.6	Chemical conversion efficiency
τ	0.015	Level of influence of abiotic environment on metabolism
T_{pref}	1000	Microbes' temperature preference

TABLE 7.7: Setup parameters

Parameter	Value	Description
M_N	100	Number of individuals in planet inoculum
B_{init}	80	Biomass of each seed individual
t_{run}	5×10^5	Duration of run (timesteps)
S_W	0.002	Probability of death by natural causes (other than starvation) at each timestep
S_F	1000	Available food required for a seed species to be viable (units)

B Supplementary material

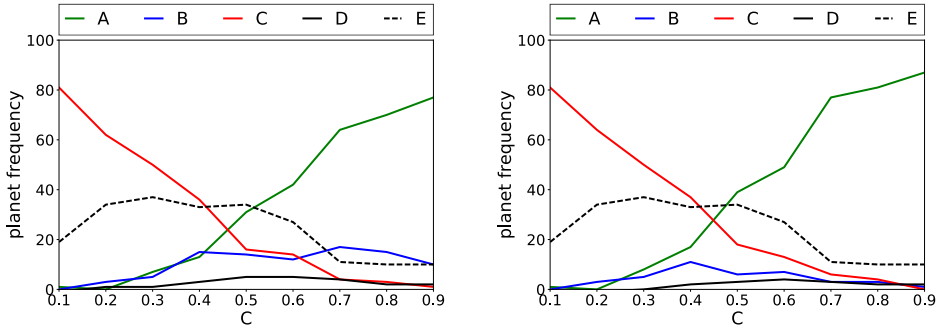
Here we present some results further exploring the ExoGaia model. These results do not change the main results of the paper but reinforce that ExoGaia exhibits self-regulation of planetary atmospheres by a microbial biosphere for a range of initial conditions.

B .1 Reseeding with life

We investigated the difference that reseeding with life had on the results. For the results presented thus far, once a system goes extinct, it remains so. We performed reseeding experiments where, after extinction, if the planet's temperature reached T_{pref} again, the planet was reseeded with a single microbe species. We did not limit the number of times a system could be reseeded. As the origins of life remain largely a mystery we don't know whether life emerged once and took off straight away, or whether it required a few starts, so investigating each scenario is of interest. Another way to think about this reseeding is that some microbial 'spores' may be so robust that they survive the crash of the system for 'geological' lengths of time (Nicholson et al., 2000) (Wells, Armstrong, and Gonzalez, 2003) (Wilkinson, 2006), however with numbers so low that they do not have any influence on the evolution of their planet. Therefore if conditions improve, life is ready to take advantage immediately. For example it is speculated that, assuming Mars once had abundant life back when it had large quantities of liquid water, life could still exist on Mars in sparse pockets 'waiting' for conditions to improve (Wilkinson, 2006). We found that the qualitative results are largely the same as for non-reseeding experiments, however survivability for all planets is improved. See Figure 7.12 for a comparison between non-reseeding and reseeding experiments.

Figure 7.12 shows the number of each Class of planets for Chemistry A both with and without reseeding. We see the most difference in the number of Bottleneck planets. For higher connectivity, we see the number of Bottleneck planets is lower for the reseeding experiment. These planets having now multiple chances for life to take hold have multiple attempts to overcome the bottleneck. This means some planets where bottlenecks were previously seen now become Abiding planets with all simulations surviving the experiment.

Some previously Doomed planets became Critical planet class under the reseeding experiment, however most remained in the Doomed classification



(A) No reseeding (B) With reseeding

FIGURE 7.12: The frequency of **A**biding, **B**ottleneck, **C**ritical, **D**oomed, and **E**xtreme planets against connectivity for chemical set A.

and those that transitioned to being critical planets were still poor long-term hosts for life, with the planet experiencing multiple reseeding events over the course of the experiment. Therefore, while some Doomed planets might, under reseeding, support life for overall longer timespans, if we consider the implications for real planets, we can infer that these planets would be unlikely to support complex life due to the frequent extinction events occurring.

B .2 Chemical Set B and C

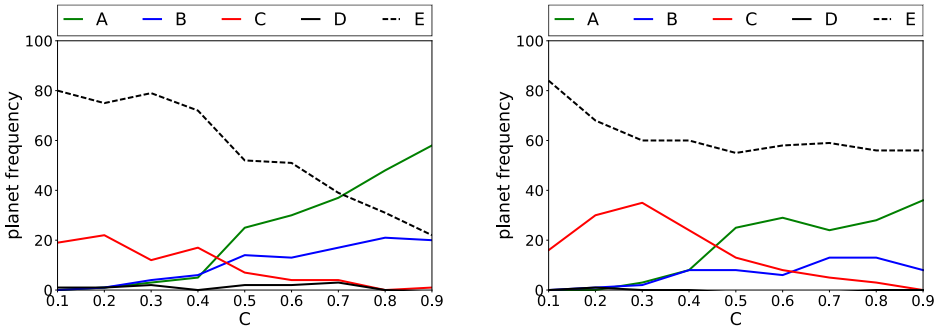
We repeated the non-reseeding experiments with two different chemical sets, to check that the results presented in the main body of the paper were not just a special case. We found that different chemical sets affect the quantitative results, but not the qualitative results of higher C correlating with higher survival rates, and Gaian bottlenecks as an emergent feature of the model. The five planet classes emerge for all three chemical sets, with the number of Abiding planets increasing with increasing C, and the number of Critical planets decreasing with increasing C. The exact number of each planet class differs between chemical sets, however the key result is that chemical set A, used for the results in the main body of the paper, is not a special case.

Table 7.8 shows the chemical species a_i values for both chemical set B and C. We can see that we would expect a planet with chemical set B to be on average warmer than a planet with chemical set C, as the chemical species are on average more insulating. Both chemical sets are significantly cooler than chemical set A. We put these two different chemical sets though the same experiments as before, investigating only the non-reseeding case. We

TABLE 7.8: The greenhouse and albedo properties for chemical sets B and Chemistry C. The bold chemicals represent the influx chemical.

Chemical index	Chemical set B	chemical set C
1	-0.56	-0.73
2	0.67	0.88
3	0.79	-0.82
4	-0.40	**0.27**
5	**0.04**	0.52
6	**0.26**	0.11
7	0.04	**-0.38**
8	-0.31	0.39
Mean	0.07	0.03

would predict that chemical set C, being colder than chemical set B, would result in fewer habitable planets.



(A) Chemistry B (B) Chemistry C

FIGURE 7.13: The frequency of **A**biding, **B**ottleneck, **C**ritical, **D**oomed, and **E**xtreme planets against connectivity

Figure 7.13 shows the number of each class of planets for chemical set B and C. We see that these quantitatively differ from one another and from chemical set A, but general trends are similar. The number of Abiding planets is highest for high *C*. Critical and Extreme planets decrease with increasing *C*, and Bottleneck planets are more common for middling and high *C* values. Doomed planets make up a very small percentage of the simulated planets for both chemical sets We find overall the colder chemical set C results in more Extreme planets, as expected. We see see that our original chemical set A, presented in the main body of the paper, is not a special case, and that viable biospheres are possible with different chemical sets.

TABLE 7.9: The greenhouse and albedo properties for chemical sets D and Chemistry E. The bold chemicals represent the influx chemicals

Chemical index	Chemical set D	chemical set E
1	**0.95**	-0.88
2	-0.70	-0.91
3	**-0.05**	**-0.43**
4	-0.39	0.94
5	-0.54	0.99
6	-0.20	-0.04
7	0.78	-0.80
8	-0.19	**-0.90**
Mean	-0.34	-2.03

B .3 Changing β_{star}

The results presented so far have $\beta_{star} < \beta_{pref}$. This means that model planets need to have insulating atmospheres to reach habitable conditions. We now investigate how changing β_{star} affects the results. We explore two cases: Chemical set D with $\beta_{star} = 1500$, therefore with $\beta_{star} > \beta_{pref}$ (instead of $\beta_{star} < \beta_{pref}$ as for chemical set A, B, and C), and chemical set E with $\beta_{star} = \beta_{pref} = 1000$. See Table 7.9 for the a_i values for the chemical species of chemical sets D and E.

We find for $\beta_{star} > \beta_{pref}$, 5 planet classes again emerge and temperature regulation can still take place. For a planet to be habitable when $\beta_{star} > \beta_{pref}$ the atmosphere must now have an overall cooling effect on the planet. In this scenario, rather than temperature regulation taking place below T_{pref} with the microbes collectively reducing the insulating power of the atmosphere to maintain habitable conditions, regulation instead takes place above T_{pref} with the microbes collectively reducing the reflective effect the atmosphere. The negative feedback loop, and the positive feedback loop are the same as outlined in Section 4.1 in the main paper but with the signs flipped such that when $T_{planet} < T_{pref}$, effects of increasing (+) the temperature are:

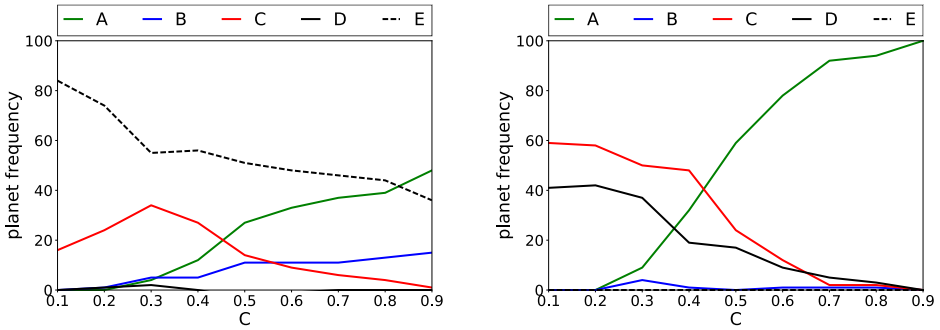
1. + Temperature $\rightarrow$ + Population
2. + Population $\rightarrow$ + Temperature

resulting in a runaway positive feedback loop. This also means decrease in T_{planet} will result in a decrease in the microbe population, further decreasing T_{planet} as abiotic processes dominate, leading to total extinction. A positive feedback loop where T_{planet} is increasing will result in $T_{planet} > T_{pref}$ where the negative feedback loop occurs, as for $T_{planet} > T_{pref}$:

1. + Temperature → -Population

2. + Population → + Temperature

resulting in a stabilising negative feedback loop. Figure 7.14 shows the frequency of each planet class for chemical set D with $\beta_{star} > \beta_{pref}$ and for chemical set E with $\beta_{star} = \beta_{pref}$. The $\beta_{star} > \beta_{pref}$ case qualitatively looks the same as the $\beta_{star} < \beta_{pref}$ scenarios for chemical set A, B, and C. All 5 planet classes are seen and as C increases the long term habitability of planets increases.



(A) Chemistry D with $\beta_{star} > \beta_{pref}$ (B) Chemistry E with $\beta_{star} = \beta_{pref}$

FIGURE 7.14: The frequency of **A**biding, **B**ottleneck, **C**ritical, **D**oomed, and **E**xtreme planets against connectivity

Figure 7.14b shows planet class frequency for $\beta_{star} = \beta_{pref}$. The behaviour of the model changes slightly under these conditions. As a planet with no atmosphere will now have $T_{planet} = T_{pref}$, the microbes, once seeded, experience a positive feedback where an increase in population leads to an increase in habitability (as the atmospheric chemicals are reduced). Thus after seeding, if habitability prevails long enough, the microbes will quickly consume all of the atmosphere. With no atmosphere the population becomes nutrient limited and temperature regulation via a negative feedback loop does not take place. Microbes maintain habitable conditions simply by preventing any atmosphere building up. This phenomena is known as biotic-plunder (Tyrrell, 2004) where the biota exhaust resources and so achieve stability, while the resources remain at very low levels. If microbe populations decrease due to stochastic fluctuations, atmospheric chemicals can build up, moving T_{planet} away from T_{pref} and leading to a positive feedback loop, resulting in extinction. For high C the temperature change is small enough that microbe numbers can recover in time to consume the excess chemicals and remain nutrient limited. For low C, where chemical species can accumulate

more rapidly, microbes are sometimes unable to prevent the positive feedback loop. Therefore we see far more Critical planets occurring for low C than for high.

There are no Extreme planets when $\beta_{star} = \beta_{pref}$. As conditions at the start of each experiment have $T_{planet} = T_{pref}$, all planets spend time in a habitable temperature range and thus all planets are potentially habitable. Doomed planets are those where T_{planet} diverges from T_{pref} too quickly before a food source has built up for microbes, preventing successful colonisation of the planet. For higher C where the chemicals are more evenly distributed between each chemical species, temperatures change at a slower rate, and thus the number of Doomed planets decreases.

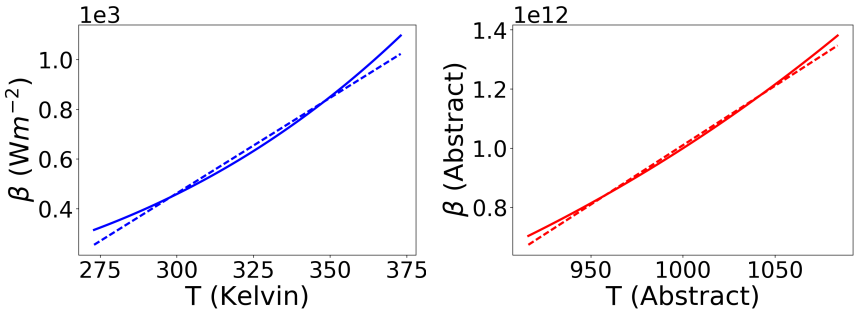
Bottlenecks are rare for $\beta_{star} = \beta_{pref}$. Previous results, Figures 6 - 10 in the main paper, showed that when microbes were seeded on a planet when $\beta_{star} < \beta_{pref}$ they caused a reduction in habitability (the same is true for $\beta_{star} > \beta_{pref}$). For $\beta_{star} = \beta_{pref}$ the sudden decrease in atmospheric chemicals due to seeding will instead lead to an increase in habitability. This prevents much of the the bottleneck behaviour seen when β_{star} is far from β_{pref}, as in Figures 7 and 8, i.e. the decrease in habitability followed by a rapid population reduction, with the population sometimes recovering and sometimes going extinct. Bottleneck behaviour can still emerge however when microbes do not evolve metabolisms fast enough to consume all chemical species building up in the atmosphere. However, with the increase in habitability after seeding, reproduction rates and thus mutation rates are higher than when β_{star} is far from β_{pref} and so varied metabolisms appear more rapidly making Bottleneck planets less likely for $\beta_{star} = \beta_{pref}$.

It seems unlikely that the biosphere on a real planet would consume the entire atmosphere, perhaps making the model results for $\beta_{star} = \beta_{pref}$ less realistic than for $\beta_{star} < \beta_{pref}$ or $\beta_{star} > \beta_{pref}$, however nutrient limitation is a well-known phenomena in ocean systems (Moore et al., 2013). The ExoGaia model demonstrates that habitable conditions can be maintained by a biosphere under a range of conditions, and we see that for each scenario tested the underlying geochemical network plays a key role in determining a planet's suitability for long term habitability.

B .4 Changing the β and T relation

The results presented throughout the main paper and this Appendix thus far have used a linear relationship between β and temperature. Figure 7.15a

shows a plot of the Stefan-Boltzmann law: $\beta = \sigma T^4$ (where σ is the Stefan-Boltzmann constant), for temperatures between $0 - 100^oC$, and a linear approximation (dashed). We can see that the linear approximation is a close fit to the T^4 curve. Figure 7.15b shows $\beta = T^4$ for the range of habitable abstract temperatures in ExoGaia: $916 - 1084$, also with a linear approximation (dashed). The T^4 relation in Figure 7.15b is slightly less curved than in Figure 7.15a however they are not vastly different. Therefore a linear approximation of $\beta \sim T$ in these temperature ranges is a close approximation.



(A) Real world habitable temperature range (B) ExoGaia habitable temperature range

FIGURE 7.15: $\beta \sim T^4$ (solid) and linear approximations (dashed) for the habitable temperature ranges for the real world (a) and ExoGaia worlds (b)

We can investigate the behaviour of the ExoGaia model with the more realistic $\beta = T^4$ instead of $\beta = T$. Multiplying T^4 by a constant, e.g. σ, is not important as this constant cancels out in the equation updating the thermal energy in a planet's atmosphere (Equation 7.16) and so can be safely ignored. Omitting σ also serves as a reminder that all temperatures in ExoGaia are abstract.

Figure 7.16 shows the frequency of each planet class against connectivity. These results use the same parameters as those used for results in the main paper, the only change being $\beta = T \rightarrow \beta = T^4$. We see that the overall behaviour of the model is unchanged, 5 planet classes emerge, with increasing connectivity correlated with increased long-term habitability success for planets. The planet class frequencies between Figure 7.16 and 7.12a (the results from the main body of the paper) differ significantly however.

The reason for this is not due to the curved β and T relation, but due to the fact that when $\beta = T^4$, doubling β no longer corresponds to doubling T. The $\beta = T^4$ relation results in far more planets being too cold for life, hence the large number of Extreme planets seen in Figure 7.16. As temperature

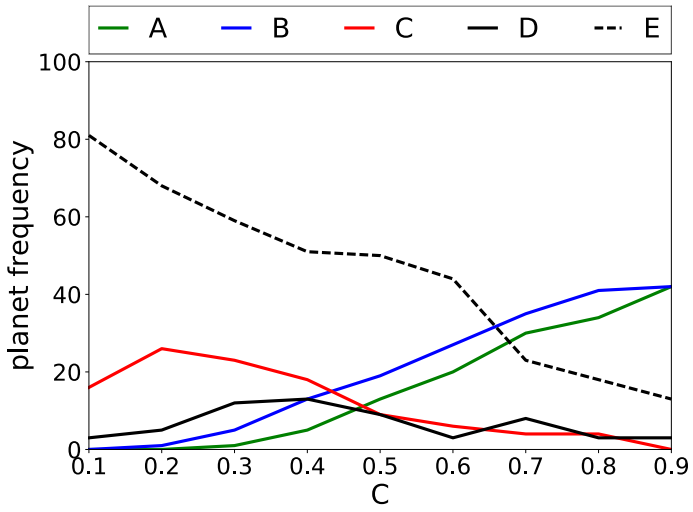


FIGURE 7.16: The frequency of **A**biding, **B**ottleneck, **C**ritical, **D**oomed, and **E**xtreme planets against connectivity for simulations where $\beta = T^4$.

in the ExoGaia model is unconstrained, fitting $\beta = A \times T^4 + B$ to approximate $\beta = T$ (to capture the curvature of a T^4 relation but maintain similarity with the original data), results in imaginary temperatures being possible – which is of course unphysical. Therefore, no fitting was performed and thus the relative planet class frequencies are quite different. However Figure 7.16 demonstrates that using a T^4 relation instead of a linear one does not impact the important results of the model, and that the model results are robust to significant changes to the β and T relationship.

Chapter Summary

This Chapter has introduced the ExoGaia model – a model of evolving microbial biospheres interacting with a simple abstract planetary atmosphere that demonstrates global regulation. The underlying biological principals of the model are the same for the flask model variants explored so far (see Chapters 4 and 5) however the environment does differ in that the atmospheric composition directly impacts planetary temperatures, as opposed to microbes influencing a global parameter via adding or subtracting a set amount as determined by their genetic code. On an ExoGaia planet life must catch a short window of habitability in order to achieve long term habitability and inhabitance. If it fails, the planet will typically quickly revert to its equilibrium state which is typically highly hostile to the model life. ExoGaia demonstrates scenarios where habitability is not possible without inhabitance, and this has deep implications for our search for alien life and habitable exoplanets. If a planet must be inhabited to be habitable it will surely impact our understanding of the so called 'habitable zone' around stars. ExoGaia also demonstrates scenarios where the same planetary setup can either rapidly become extinct of all life and move to an inhospitable state, or have life successfully become established and maintain long term habitability.

In ExoGaia, the underlying geochemical network is very important in predicting how easily life will be able to colonise a planet, and maintain habitable conditions once established. ExoGaia predicts that planets that are very active geochemically, with many pre-made recycling loops already established for life to insert itself into, would be better candidates for long term habitability. Model planets with an equilibrium temperature (a planet devoid of life with its atmosphere in chemical equilibrium) that is habitable, turn out to be poor hosts of life. All life must interact with its environment and in ExoGaia microbes must consume chemicals in their atmosphere to survive, and in doing so they will then change the planetary temperature as they alter the atmospheric composition. Therefore, if temperatures without life would have been nearly ideal, any action by life will clearly degrade the environment. This again has implications for our search for inhabited planets.

ExoGaia is such an abstract simple model that I don't want to suggest that I think these results are directly applicable to the Earth or to any other planet we might want to consider, however these results do strongly add to the hypothesis that habitability and inhabitance are two sides of the same coin (Goldblatt, 2016).

Chapter 8

Discussion

The Gaia Hypothesis postulates that life and the oceans, crust and atmosphere of Earth form a self-regulating planetary-scale system with stabilising properties that help explain the long uninterrupted history of life on Earth. This thesis has explored the Gaia hypothesis, the history of its formulation, and how the hypothesis can help us understand life's long persistence on Earth in the face of perturbations such as our ageing sun, and how life might dramatically alter the physical evolution of a planet, to catch a window of habitability and maintain it, as demonstrated with the ExoGaia model.

1 Summary

In this thesis I have given a brief account of the long history of our Earth in Chapter 1, covering events most relevant to the emergence of the world we see today. I then outlined the history of the Gaia hypothesis in Chapter 2, and gave an overview some of the key existing Gaian models and the various mechanisms whereby self-regulation can emerge in a life-environment coupled system (Chapter 3). In Chapter 4 I presented a new variant of the Flask model that exhibits a new method of self-regulation not before described - single rein control. In Chapter 5, I explored the hypothesis of 'selection by survival' and demonstrated that this selection mechanism can have a strong influence on the persistence of self-regulating biospheres. This model demonstrated the importance of starting conditions on a 'planet' when life emerges. The further conditions are from 'ideal' for life, the harder it is for early life to become and established biosphere. This early stage of life colonisation in these models is the most dangerous time for life. However if life manages to become established, biospheres with self-regulating feedback loops will then have a greater chance of long term persistence than those that don't.

In chapter 6 I discussed the search for alien life and habitable exoplanets focusing on the histories, and potential past habitabilities, of Earth's two neighbouring planets - Venus and Mars. In chapter 7 I then introduced the ExoGaia model - a model of atmospheric regulation by an evolving microbial biosphere. While still highly abstract this model was designed to more accurately mimmic how life interacts with Earth's atmosphere than the other models described in this thesis. In the models of chapters 4 and 5, life influenced parameters by adding or subtracting set amounts as they converted food to biomass as a metabolic byproduct. In ExoGaia instead the food is the atmosphere, just as we depend on O_2 and photosynthetic life depends on CO_2. Within ExoGaia single-rein control emerges as a regulation mechanism, with life acting to counteract runaway greenhouse warming that would occur on a planet devoid of life. The ExoGaia model also demonstrates how important the underlying geochemistry of a planet might be for long term habitability. On a planet were there are already closed feedback loops formed by the geochemistry, biology can quickly and easily act to amplify these existing feedback loops to regulate their environment. On planets where certain atmospheric gases are prone to build up in an uncontrolled manner without the action of life, habitability is less assured and the planet can be prone to large temperature fluctuations which come with a risk of extinction.

2 Conclusions

I will now present a summary of the conclusions I have drawn based on my work in this thesis, and my reading on the vast array of topics that constitute the notion of Gaia. Firstly I will address the title of this thesis.

2 .1 Mechanisms that have produced a self-regulating Earth system.

In this thesis I have covered a number of self-regulation and selection mechanisms which all likely play a role in forming the living Earth system. The majority of the work presented in this thesis has focused on the regulation mechanism 'single-rein control', and the hypothesis of 'selection by survival'.

Single-rein control

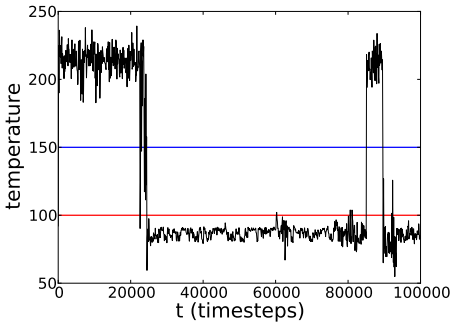
In Chapters 4 and 7 (and to some extent in Chapter 5) I have shown how an evolving microbial biosphere can regulate a globally shared environment in

the absence of niche construction, or any form of individual or group selection for regulation. In models that exhibit single-rein control, all microbes share the same 'ideal' conditions where their fitness is at a maximum. The mechanics of this regulation mechanism are simple - if conditions are habitable, life will reproduce and the population will grow, if conditions are poor, life will die and the population will shrink. This growing and shrinking of the population will change life's impact on its environment.

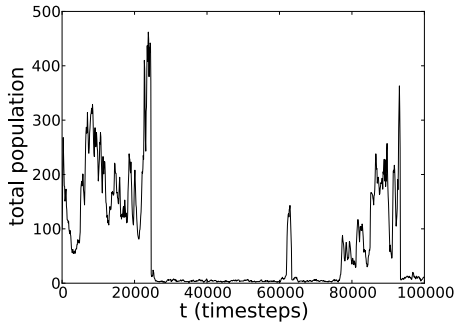
Single-rein control is not as simple as having environment-improving biospheres and environment-degrading ones. A perturbation on the environment by life might initially be environment-improving, however pushing the environment too far in any direction will eventually lead to environmental degradation. Thus even environment-improving biospheres will tend to become self-limiting (unless first limited due to some other factor, e.g. resource limitation). It is exactly this self-limiting behaviour which allows for the single-rein control mechanism to emerge and regulate global parameters. Temperature regulation occurs at the point where the reproduction rate of microbes is equal to the death rate.

In the single-Flask model (Chapter 4), the microbes affect the temperature (and thus the habitability) of their shared global environment as a by-product of their metabolism. The temperature of the system is represented as a parameter which is independent of the nutrient availability of the system. The microbes' impact on temperature is also decoupled from which nutrients they eat and excrete. Two species might consume and excrete the same nutrients, but have very different impacts on temperature. Under these conditions when a mutant arises the single-rein control mechanism adjusts the total population to keep the overall impact exerted by the biosphere on its abiotic environment constant. This effectively maintains an, on average, constant fitness for life by 'tuning' the population to a suitable level. The population can fluctuate wildly during a regulated regime depending on how the microbe community changes. The nutrients life depends on for food in the single-flask model (and most other flask model variants) have no impact on the global temperature that impacts microbial fitness, therefore regulating the global temperature, and establishing nutrient recycling loops to avoid exhausting food resources are two independent problems for life to solve. The abiotic flask environment is set to be habitable when at equilibrium and life can then perturb the environment to regulate either above or below its ideal temperature. Rapid transitions between these two regulation regimes occur

where mutants appear that shift the overall impact of the microbe community on the environment from cooling to heating, or vice versa, Figure 8.1.



(A) The temperature of a single-Flask system.

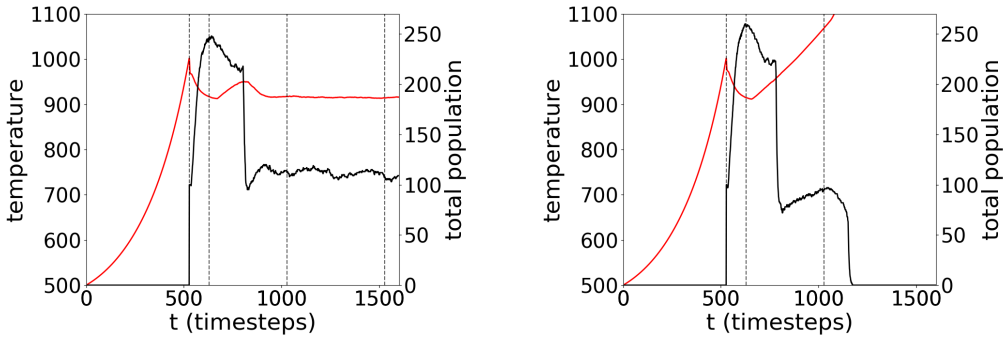


(B) Corresponding total population over time for the same system.

FIGURE 8.1: These graphs show the two temperature regulation regimes that emerge from the single-flask model. Both demonstrate single-rein control. These figures show how the total population of the system can vary dramatically during temperature regulation. In Figure (A) red indicates the abiotic temperature of the system, and blue indicates the 'ideal' temperature for life. Temperature regulation occurs symmetrically above and below this 'ideal' temperature.

In the ExoGaia model (Chapter 7) the population experiences less fluctuation under single-rein control. In ExoGaia, the food consumed and the waste excreted by life are components of the planet's atmosphere. Therefore the impact life has on its environment is not represented by adding or subtracting a set amount to a global parameter as in the Flask model, but on the impact life has on the atmospheric composition. To maintain a habitable temperature in ExoGaia, life must maintain a suitable atmospheric composition to provide sufficient warming, while preventing overheating as planets without life in ExoGaia will usually quickly revert to an inhospitable state due to the build up of greenhouse gases, Figure 8.2.

In ExoGaia it is again the collective actions of the biosphere which lead to regulation, there is no mechanism by which microbes which consume greenhouse gases can be naturally selected for over those that consume cooling gases. If conditions improve for one species, they improve for all, and so a balance will be found where the microbes' collective impact on the atmosphere results in a habitable temperature. For a stable temperature, the atmospheric composition must itself remain near constant, and so the population of an ExoGaia biosphere is set to the population that consumes any additional gases input to the atmosphere due to abiotic processes once the stable



(A) Successful colonisation of an ExoGaia planet.

(B) The same planet where life failed to become established.

FIGURE 8.2: These graphs show two experiments for a 'bottleneck' ExoGaia planet, one where life successfully colonised its planet and established temperature regulation, and one where it failed, and the temperature of the planet rapidly increased to inhospitable levels. Red indicates the temperature of the planet, black the population of the biosphere. In Figure (B) we can see that without the influence of life, the temperature will quickly rise to an inhospitable level. The ideal temperature for life is set to 1000 in these experiments.

regime has been found. Therefore in ExoGaia the population of the biosphere is often much more stable than for the single-Flask model, and population fluctuations correspond directly to fluctuations in the atmospheric composition and thus the temperature of the planet.

The abiotic environment at equilibrium in the single-flask model is set to be habitable to life, however in ExoGaia, the equilibrium state of a planet is often inhospitable; life has a narrow window of habitability within which to become established. In the majority of ExoGaia experiments, the planet requires an insulating atmosphere for habitable temperatures to be reached. This means that any biosphere will act to cool its environment, as any general consumption of the atmosphere will lessen its insulating power. Therefore only one regulating regime emerges in ExoGaia.

The single-rein control regulation mechanism is similar to the 1-daisy-type Daisyworld model described in Watson and Lovelock (1983). In this version of Daisyworld only black or only white daisies exist on the planet, and therefore the habitability of the Daisyworld planet is identical for all possible lifeforms. The community of purely black, or purely white, daisies must adjust to maintain a habitable temperature in the face of a warming host sun. This is single-rein control involving only one species, only differing in that local space is a property of the Daisyworld model which is absent in the models exhibiting single-rein control described in this thesis.

The single-Flask model and the ExoGaia model show how single-rein control can work in two different scenarios. ExoGaia might demonstrate how life plays a role in regulating our atmosphere and thus planetary temperatures to maintain habitability. However as life requires more than a habitable temperature to thrive, and factors such as salinity and pH are also important, single-rein control as demonstrated in the single-Flask model is likely to play a role where life is interacting with many aspects of its environment at once that are not necessarily dependant on one another, for example nutrient availability and soil pH impacting plant growth. This aspect of single-rein control could also be used as an analogy of our current global crisis. The carbon footprint of the average human on Earth today is causing global warming. To stabilise our impact on the planet either the human population or our average impact on the planet must reduce. As the former would necessitate a huge cost in human life, the latter must be the option we choose.

Selection by survival

On the face of it, 'selection by survival' perhaps doesn't appear to add much to the Gaian debate. Of course systems that survive, survive. Natural selection might also at first have been seen to also be stating the obvious; of course 'the fittest survive', yet this basic mechanism has fundamental importance to evolution. Regarding Gaia, it has often been suggested that we should largely expect 'anti-Gaian' biospheres over 'Gaian' ones, after all there are more ways to destabilise than to stabilise a planet. Selection by survival helps explain why we should expect Gaia to be favoured over anti-Gaia when looking at planets that host life. Quite simply, those that survive will be those that have self-regulatory mechanisms, and the longer these systems survive, the more chance they have to acquire further persistence enhancing properties. Therefore we would expect a universe to contain 'Gaian' inhabited planets and lifeless planets, but not planets hosting 'anti-Gaian' biospheres.

The work presented in Chapter 5 shows that selection by survival does have an influence on the survival prospects of life-environment coupled systems over a null hypothesis of a constant chance of extinction, see Chapter 5 where these planets are imagined as independent single flask worlds. Flask worlds can reduce their chances of experiencing an extinction event by improving their environment towards an 'ideal', however none of the biosphere components are in any way aware of these looming extinction events. They all are acting as in earlier models, obliviously living their lives and reacting

to, and shaping, the environment they find themselves in. Yet those Flask systems were self-regulation emerges can have enhanced survival prospects.

Selection by survival was presented as a way to unite Darwinian selection and the Gaia hypothesis by allowing for selection for Gaia and removing the problem posed by considering Gaia under Darwinian terms of "how can self-regulation be selected for". There are no competing biospheres. However, although I do think selection by survival plays a role in understanding the formation and persistence of a Gaian system (other models, e.g. the Tangled Nature Model have noted before that persistent systems are statistically likely to further persist) I do not think Gaia needs to be explained in Darwinian terms. Yet Gaia and natural selection must be compatible, which many have thought to not be possible, a point which leads me to the next section.

An entropic mechanism for Gaia

Many Gaian models have now demonstrated self-regulation emerging out of the collective actions of the biosphere, the individuals of which are subject to natural selection. Pressure on selection for a self-regulation at the level of the planet is not required for self-regulation to robustly emerge. Although natural selection and the Gaia hypothesis cannot be contradictory, Gaia need not be explained in terms of Darwinian selection, and indeed that trying to do so may hinder understanding of the emergent nature of Gaia. Model microbes in a shared environment, reacting only to their own environmentally determined 'fitness' levels, can produce robust environmental regulation as demonstrated by numerous models, including the ones presented in this thesis. In the same way the consciousness of you or I cannot be fully understood by looking at neurons, Gaia cannot be fully understood by only observing parts of her in isolation. If we pulled apart these models and looked at the composite parts, it probably wouldn't be obvious that self-regulation would emerge. It is only by looking at the system as a whole that this self-regulating property of the system can be understood. It is the full system that constitutes Gaia. These Gaian models demonstrate that Gaia can more easily be understood as an emergent statistical property, rather than using reductionism (Lovelock, 2003). In the same way that 'temperature' only emerges on the macro scale (atoms / molecules have energies, not temperatures), Gaia only emerges when looking at the large-scale and long-term interactions between life and the planet.

In Chapter 3 I briefly covered a variation of the Tangled Nature Model (TNM), which neatly demonstrates an entropic argument for Gaia (Arthur and Nicholson, 2017). The original TNM (Christensen et al., 2002) was designed to answer questions based on trends in the fossil record - why has there been a trend towards increasing diversity (Benton, 1995), and increasing stability over time (Newman and Sibani, 1999; Newman and Eble, 1999)? The TNM demonstrated that these phenomena are emergent results of 'tangled' ecosystems co-evolving, with collapses of ecosystems and new ones forming, over time. The reason for increasing ecosystem complexity is the same as for the bag of cables example in Chapter 2 - there are more configurations for more diverse ecosystems than there are for simpler ones. Therefore over time, a more diverse ecosystem is statistically more probable than a simpler one. The trend in increasing stability of ecosystems is due to the higher entropic barrier presented by a larger more diverse ecosystem than a simple one. It's easier and faster to untangle two cables than it is five.

I think that understanding this mechanism is key to understanding Gaia. Life in this model, as in all Gaian models, impacts its environment and can have either a positive or negative impact on habitability. This model is characterised by quasi-stable ecosystems, with well defined 'core' member species, punctuated by rapid periods of fluctuation, known as 'quakes', triggered usually by the appearance of a rapidly reproducing mutant. During a quake, as the population of each species existent at that time are so low, any environmental impacts species have are near negligible. Inter-species interactions are far more important in this early stage of ecosystem formation. Therefore if we took a Darwinian view to this, we would be puzzled at how to explain why on average, over time, ecosystems tend to improve their environment rather than degrade, and that this environment improvement also increases over time. Environment improving traits are not being selected for in the early stages of the formation of the ecosystem, and these impacts on habitability only really kick in once an ecosystem is established.

An entropic understanding clarifies things. Simply put, environment-degrading ecosystems self-limit, resulting in smaller populations and are highly susceptible to destabilising mutants. Therefore the lifetime of these ecosystems tends to be short. In contrast, environment-improving ecosystems enjoy a higher populations and are far more resilient to the appearance of mutants. These ecosystems therefore tend to survive far longer before collapsing. Therefore on average, for later times we expect to find the system in a longer lived environment-improving ecosystem. The system will

reconfigure via 'sequential selection' through, possibly a few, environment-degrading ecosystems that are self-limiting and short lived, before chancing on an environment-improving ecosystem, which can then reach a larger population and enjoy longer term survival prospects. If these ecosystems are longer lived, we expect the system to spend more time in such configurations. Therefore even in the absence of any selection for environment-improving ecosystems, they are the expected state of an older system. The Earth-life coupled system has been around at least 3.8 billion years. That's a long time! We have identified numerous self-regulation mechanisms at work on the Earth. The entropic argument says that it is statistically likely that we would find the Earth, after over 3 billion years, in a habitable and inhabited self-regulating state hosting a diverse and populous biosphere.

Gaia across multiple scales

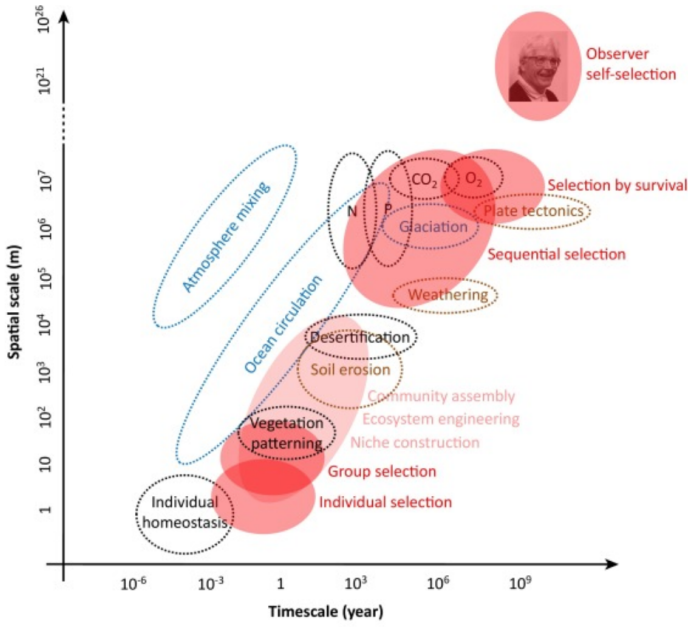


FIGURE 8.3: This figure, from Lenton et al. (2018) shows some key Earth system processes, with feedback mechanisms and some regulated variables shown in black, and selection mechanisms shown in red. Other important Earth processes, such as ocean mixing, are shown in blue and brown.

As mentioned in Chapter 3, there are many more identified selection and self-regulation mechanisms that emerge from Gaian models, and are likely playing a role in the self-regulation of Earth, than have been explored in detail in this thesis. Lenton et al. (2018) (a paper on which I am a co-author) provides a nice summary of the varying timescales and spacial scales that

selection mechanisms work across, shown in Figure 8.3. This diagram shows part of the complex answer to the question posed in this thesis' title. Multiple selection mechanisms at work at all scales of our Earth system, from the level of an individual organism, to the level of the whole planet, have been important in forming Gaia. The regulation mechanisms explored in this thesis, namely rein control and single rein control will be at work at multple scales, from regulating my blood sugar levels (Saunders, Koeslag, and Wessels, 1998), to potentially playing a strong role in regulating planetary temperatures.

2 .2 The case for a Probable Gaia

In Chapter 2, I introduced several variants of the Gaia hypothesis as defined by Kirchner (1989):

Coevolutionary Gaia Life influences its abiotic environment, and the environment in turn influences life.

Homeostatic Gaia Life influences the world in a way that leads to stability due to the dominant links between life and the abiotc world being negative feedback loops.

Geophysiological Gaia The biosphere-planet coupled system can be described as a single organism, which can exhibit both homeostatic and unstable behaviour, like other organisms.

Optimising Gaia Life interacts with its physical environment in such a way to optimise conditions for life at any point in time.

with Homeostatic Gaia being further broken down into:

Lucky Gaia The Earth has homeostatic properties largely by luck (Watson, 2004).

Probable Gaia The probability for a life-planet coupled system to develop homeostatic properties is greater than the probability to evolve non-homeostatis (Lenton and Wilkinson, 2003).

I believe that previous models combined with the work in this thesis, present strong evidence for 'Homeostatic Gaia'. Not only that, but for a 'Probable Gaia'. Models such as Daisyworld, Daisystat, Guild model, Flask world, single-Flask world, Greenhouse world, and ExoGaia all exhibit self

regulation based on simple ground rules. There is no ability for organisms within these models to collectively decide and aim for the environment they'd like. Via their own self-interested actions within their environments self-regulation robustly emerges in many modelled life-environment coupled systems, and shows resilience to perturbation, both internal and external. These models have included systems with a number of different spatial structures, allowing niche construction (e.g. the Guild model (Downing and Zvirinsky, 1999)) and group selection (e.g. variants of the Flask model (Williams and Lenton, 2008)), and also models lacking any spatial structure, and therefore preventing these phenomena (such as the models presented in Chapters 4, 5 and 7 of this thesis). Models have explored biospheres allowing for adaptation to prevailing conditions e.g. the Daisystat (Dyke, 2010), and also fixed environmental requirements e.g. ExoGaia (Chapter 7). Many of these models allow for "cheats" - species that would benefit from the environment-improving actions of others while not contributing themselves, and have found that regulation is not destroyed. The Tangled Nature Model variant adapted to explore Gaia (Arthur and Nicholson, 2017) found that entropic hierarchies lead the system to favour increasing environment-improving biospheres over time. The large diversity in models exhibiting robust self-regulation as an emergent feature is evidence that self-regulation is an expected property of a life-environment coupled system, not an exception. It suggests that the emergence of Gaia is probable, not lucky, and that Gaia plays a strong role in explaining the continued habitability and inhabitance of planet Earth.

2 .3 ExoGaias

The Gaia hypothesis has strong implications for our search for extraterrestrial life. If Probable Homeostatic Gaia is correct, then self-regulating biospheres should be a feature of the universe and not an exception (with the assumption that the probability of life emerging is not vanishingly small). However all models exhibiting self-regulation have requirements to allow for that self-regulation to emerge in the first place. Conditions must be initially habitable, allowing early life to proliferate, and life of course, must appear. These are both huge unknowns in our current understanding of the universe. These models also assume an abundant energy source for any life that should emerge (e.g. sunlight), and suitable terrestrial worlds for them to

emerge onto. The highly abstract models presented in this thesis make concrete conclusions impossible, however the results can inform our searches for inhabited exoplanets.

In the ExoGaia model (Chapter 7) we saw that an initially habitable temperature was not enough to secure long term habitability on a planet - the underlying geochemistry played a strong role in determining how successful a biosphere would be in becoming established and maintaining habitable conditions. In ExoGaia, a planet might reach habitable temperatures and thus allow for the emergence of life, however the long-term habitable prospects of the planet strongly depend on the underlying geochemistry. Planets with an abundance of geochemistry (many abiotic recycling loops), had much higher probabilities of becoming colonised with life and maintaining habitable conditions for long timespans, than those without. On top of that, the conditions on inhabited planets in the ExoGaia model are often vastly different to those same planets in the absence of life.

The ExoGaia model predicts that geochemically / geologically active planets will have better habitability prospects than those without. This is a testable hypothesis. Lenardic and Seales (2019) argue, correctly to my mind, that when searching for habitable exoplanets 'different is more'. They warn against focusing the search for planets that remind us of Earth, and argue that in our goal to answer how widespread life might be in the universe, looking at planets that differ significantly to Earth will help us more in finding answers. Finding life on an Earth-like planet would be an astounding discovery, but finding life on a planet that differs significantly from Earth would immediately demonstrate that Earth-like properties are not a prerequisite for life. It immediately would give us more information on how abundant we expect life to be in the universe. One example of a planet that would differ significantly to Earth given in Lenardic and Seales (2019) is a terrestrial planet lacking plate tectonics. ExoGaia would predict this to be a poor candidate for life. But we're not going to know unless we find such planets and observe them in detail. Clearly there are many planets that will fall outside the scope of ExoGaia, such as water worlds, planets with 10 - 100 times the water on Earth. These are predicted to allow for habitable conditions without the requirement of geochemical recycling (Kite and Ford, 2018). On such planets ocean currents are thought to be able to replace much of what geochemistry achieves on Earth in terms of forming abiotic recycling networks. I strongly agree with the "different is more" philosophy of searching for life. Experimental verification of any hypothesis on planetary habitability require us to

observe many different types of planets, not just Earth-like ones.

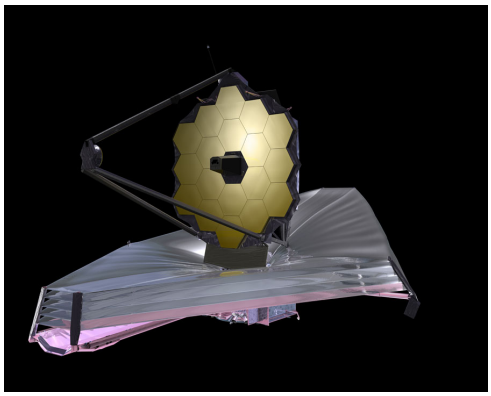
The ExoGaia model predicts that habitability and inhabitance are largely inseparable. This is a concept explored in Goldblatt (2016) as “the inhabitance paradox". And this has strong implications for how we understand concepts such as the habitable zone, as put clearly in a quote from Goldblatt (2016):

> “... the habitable zone seeks to define the region a planet should be capable of harbouring life; yet whether the planet is inhabited will determine whether the climate may be habitable at any given distance from the star."

In ExoGaia, the majority of planets that enjoy long term habitability, would only remain habitable for brief periods of time without the influence of life. Life must quickly emerge and establish itself to prevent the abiotic processes from driving the planet to an inhospitable state. The example focused on in Chapter 7 was whether a lifeless Earth might look like Venus, or whether a Venus with a biosphere might have avoided its present-day scorched fate, and looked more like Earth today. Are Venus and Earth alternate states of the same system? Did our planet survive a “Gaian Bottleneck" (Chopra and Lineweaver, 2016), where life must quickly establish self regulation to survive, or face extinction, and did Venus’s early biosphere (imagining that it had one) fail this crucial step?

In the ExoGaia model, the vast majority of simulated planets that had habitable temperatures when their atmospheres were in chemical equilibrium, were actually inhospitable to life. Life, by living, interacts and changes its environment. Therefore in these model environments where there is a fixed ‘ideal’, if the conditions are already at this optimum, any action by life will degrade the environment. It is therefore easier for life to maintain habitable conditions on a planet as it passes through a brief period of habitability (assuming life can ‘catch’ this crucial stage) than for life to persist on an apparently ‘perfect’ planet which is at chemical equilibrium. This suggests that we may need to look outside the traditionally defined habitable zone in our search for alien life. This again is a testable hypothesis. With the James Webb telescope (due to be launched in 2021) we will be able to analyse the atmospheric composition of various planets, and thus look for biomarkers. Should we find such signatures, or indeed tolerable surface temperatures, where our models predict otherwise, this could be more evidence for habitability and inhabitance being two sides of the same coin. We would then have to ask what the likelihood of early life surviving the “Gaian Bottleneck” is. If we

take Probable Homeostatic Gaia as our working hypothesis, then assuming a suitable planet and the emergence of life, we would expect a large percentage of biospheres to survive this bottleneck.



(A) Artists impression of the James Webb Space Telescope deployed.

(B) Artists impression of the proposed Europa Lander. Ir would search for evidence of life on Europa.

FIGURE 8.4: Exciting planned future mission promise to give some answers to our questions regarding alien life. Is there life under Europa's icy surface? Can we find evidence of alien biospheres in the atmospheres of distant planets? Image credits: NASA

The predictions of the ExoGaia model suggest that when looking at exoplanets, the age of the solar system will determine what we expect to find in terms of alien life. For a young newly-formed system, perhaps there will be abundant early life on many planets, as is thought to have been possible early on in the formation of our own solar system. It's possible that early Venus and Mars were also habitable if not inhabited back when life emerged on Earth. It's even speculated that life on Earth might have Martian origins (Davis and McKay, 1996; Davies, 2004). For older systems however, if the hypotheses of Gaian bottlenecks, and inhabitance and habitability being tightly coupled are correct, we would expect to find either old well-established life, no life, or perhaps sparse pockets of bacterial-like life clinging onto survival as a relic of a once vibrant biosphere. In older fully-formed solar systems we would not expect new life to start appearing. Combined with the entropic arguments for Gaia we can form a bolder hypothesis, that not only would we expect this life to be old and well-established, but also to be a diverse and complex biosphere which has improved, not just maintained, habitability prospects on its planet.

The next few decades promise to be very exciting for exoplanet and alien life research. It's quite possible we could start to have some answers to the

question that has been asked for thousands of years: Are we alone in the universe?

3 Future work

There is still much to be understood about our living planet. What is the relative importance of each regulation mechanism identified in this thesis for Earth's continued inhabited state? How resilient are those regulation mechanisms in the face of perturbation, especially the climate change caused by human activities? For understanding the probability of Gaia, looking to other planets will help answer some of our questions. Much of that work lies in engineering new telescopes, and robotic missions for exploration. But in turn the data they acquire could inspire the generation of Gaian models.

There is large scope for expanding the ExoGaia model. Perturbations of various types (mimicking changes in geological activity over time for example) could be incorporated into the model, as could more realistic chemistry. Currently as the model stands it is highly abstract, making relating results from the model to Earth difficult. Using a more realistic chemistry could perhaps tell us which of the habitable planet classes emergent from the ExoGaia model (Critical, Bottleneck, or Abiding) the Earth is. Currently ExoGaia is a zero-dimensional model, and so geographical space could be added to the model to consider how this might impact planetary regulation. Models of daisyworld variants have found that adding space to models can dramatically impact regulation. On Earth, local temperatures can vary dramatically, impacted strongly by the spherical shape of our planet and the differing levels of sunlight falling at different latitudes throughout the year. How would the behaviour of the ExoGaia model change if microbial life experienced different fitness depending on where they lived on their planet? How would the model behaved if microbes could move and colonise uninhabited grid-spaces, or perhaps outcompete already existent ecosystems?

On Earth, the albedo of the planet, and therefore the ice coverage, plays a strong role in determining our climate. Runaway glaciation or ice melting can lead to dramatic rapid (in geological timescales) changes (e.g. the Snowball Earth's explored in Chapter 1). This phenomena is also missing from the ExoGaia model, which only considers life interacting with an atmosphere, and does not consider further impacts a changing temperature might have

on other properties of the planet. One option would be to add biotic elements to abiotic models designed explore oscillations in Earth's ice coverage and temperature over time, for example the model presented by Kroll (2017).

Elements of the Gaian Tangled Nature Model (TNM) (Arthur and Nicholson, 2017), namely the inter-species interactions, could be combined with an ExoGaia like chemical atmosphere that these species now must consume to survive, replacing the abiotic carrying capacity parameter present in the original TNM. In ExoGaia, once the microbe community has established regulatory feedback loops and stabilised its planet's temperature the microbe population cannot experience any further growth as the chemical input to the system limits the carrying capacity of the system. If interspecies interactions are included, and the possibility of further population growth is present, how might this affect the regulation seen in ExoGaia? How would the quakes that characterise the TNM as one ecosystem collapses and a new one forms impact the biosphere's atmospheric regulation?

There is work happing in Exeter University currently to combine biotic feedback with highly realistic exoplanet climate models based on the MetOffice's global circulation model called the Unified Model. This is an exciting step and could help determine possible bio-signatures for other planets, or help predict boundaries for an 'inhabited' habitable zone, as we could measure the impact life might have in keeping a planet habitable outside the traditionally defined habitable zone. Models such as the one presented in Kharecha, Kasting, and Siefert (2005) use realistic biogeochemistry to understand Earth's climate history, and similar models used instead to predict possible future climates for planets, rather than focusing on recreating a specific past climate, could help further test the hypothesis of 'Gaian bottlenecks' (Chopra and Lineweaver, 2016). Another model developed by Gebauer et al. (2018) explores the atmospheric evolution of planets orbiting M dwarf to investigate implications for bio-signatures on such planets where key life-processes on Earth, such as photosynthesis, may be different.

4 Closing thoughts

I have written and rewritten these closing thoughts many times as nothing seems quite fitting. In this thesis I have focused on abstract computer models designed to better understand our living planet and they have mostly focused on early life on a new planet - the beginning and maintenance of habitable conditions. Today however, in the real world, our planet is headed

towards a crisis and I can't write a whole thesis on Gaia without at least a mention on what we are doing to our home. The oceans are filling with plastic, our world is warming, forests are disappearing, species are going extinct at truly alarming rates due to our activities (Pimm and Raven, 2000; McKee et al., 2004; De Vos et al., 2015). Anthropogenic climate change is estimated to claim 150,000 human lives annually (Patz et al., 2005; Haines et al., 2006; Williams, 2008) and those who contribute least to climate change are far more at risk of its consequences (Bank, Mearns, and Norton, 2009). Most alarming is that we have known about this danger for decades, and yet still very little action has been taken. We have been a part of this planet for less than 0.05% of its long history. Given that fact it seems truly bizarre to me that we feel we can try to dominate and rearrange the planet to suit our whims, ignore the very clear warning signs that we are approaching disaster (for ourselves anyway, microbes have powered through the great oxidation and Snowball Earth events), and yet still appear to think we'll somehow be okay continuing with 'business as usual'. Thankfully in the face of overwhelming lack of action from our politicians, everyday people have begun to speak out and refuse to be ignored.

At the time of writing these words the group 'Extinction Rebellion' succeeded in shutting down major parts of London such as Oxford Circus, Parliament square and Waterloo Bridge in protest at the UK government's lack of action on climate change. People were suddenly able to walk on major London roads usually dominated by traffic. Air pollution quickly and dramatically fell in places where vehicles were barred. Without the constant noise of cars drowning them out birds could be heard singing in central London for the first time in decades (Perraudin, 2019). There was singing, dancing, speeches and music. People from all walks of life stopped and talked to each other in a city world famous for its unfriendliness. In forcing the capital to slow down something beautiful emerged. In such moments I see hope for the future and a rekindling of our relationship with Gaia.

Bibliography

Abe, Yutaka et al. (2011). "Habitable Zone Limits for Dry Planets". In: *Astrobiology* 11.5, pp. 443–460. DOI: 10.1089/ast.2010.0545. URL: https://doi.org/10.1089/ast.2010.0545 (pages 145, 149).

Abramov, Oleg and Stephen J. Mojzsis (2009). "Microbial habitability of the Hadean Earth during the late heavy bombardment". In: *Nature* 459, 419 EP –. URL: https://doi.org/10.1038/nature08015 (pages 6, 8).

Ackland, Graeme J., Michael A. Clark, and Timothy M. Lenton (2003). "Catastrophic desert formation in Daisyworld". In: *Journal of Theoretical Biology* 223 (page 40).

Adams, B. and J. Carr (2003). "Spatial pattern formation in a model of vegetation-climate feedback". In: *Nonlinearity* 16.4 (pages 39–41).

Alemseged, Zeresenay, Yves Coppens, and Denis Geraads (2002). "Hominid cranium from Omo: Description and taxonomy of Omo-323-1976-896". In: *American Journal of Physical Anthropology* 117.2, pp. 103–112. DOI: 10.1002/ajpa.10032. URL: https://doi.org/10.1002/ajpa.10032 (pages 9, 20).

Anbar, Ariel D. et al. (2007). "A Whiff of Oxygen Before the Great Oxidation Event?" In: *Science* 317.5846, p. 1903. URL: http://science.sciencemag.org/content/317/5846/1903.abstract (page 13).

Anders, William and NASA (1968). *Earth Rise*. https://www.hq.nasa.gov/office/pao/History/alsj/a410/AS8-14-2383HR.jpg (page 24).

Andersen, Christian Walther and Paolo Sibani (2016). "Tangled nature model of evolutionary dynamics reconsidered: Structural and dynamical effects of trait inheritance". In: *Physical Review E* 93.5, pp. 052410–. URL: http://link.aps.org/doi/10.1103/PhysRevE.93.052410 (page 70).

Anderson, Paul E. and Henrik Jeldtoft Jensen (2005). "Network properties, species abundance and evolution in a model of evolutionary ecology". In: *Journal of Theoretical Biology* 232.4, pp. 551–558. DOI: https://doi.org/10.1016/j.jtbi.2004.03.029. URL: http://www.sciencedirect.com/science/article/pii/S0022519304004229 (pages 51, 57).

Arthur, Rudy and Arwen E. Nicholson (2017). "An entropic model of Gaia". In: *Journal of Theoretical Biology* 430, pp. 177–184. DOI: https://doi.org/

10.1016/j.jtbi.2017.07.005. URL: http://www.sciencedirect.com/science/article/pii/S0022519317303302 (pages 51, 53, 54, 60, 158, 224, 227, 232).

Ashby, W. Ross (1960). "The Homeostat". In: *Design for a Brain: The origin of adaptive behaviour*. Dordrecht: Springer Netherlands, pp. 100–121. ISBN: 978-94-015-1320-3. DOI: 10.1007/978-94-015-1320-3{_}8. URL: https://doi.org/10.1007/978-94-015-1320-3_8 (page 45).

Baker, B.W. and E.P. Hill (2003). *Beaver (Castor canadensis). Wild Mammals of North America: Biology, Management, and Conservation. Maryland*. The Johns Hopkins University Press (page 31).

Bangs, Edward E (1996). "Reintroducing the gray wolf to central Indaho and Yellowstone National Park". In: *Wildl Soc Bull* 24, pp. 402–413 (page 31).

Bank, World, Robin Mearns, and Andrew Norton (2009). *The Social Dimensions of Climate Change*. The World Bank, p. 319. ISBN: 978-0-8213-7887-8. DOI: doi:10.1596/978-0-8213-7887-8. URL: https://doi.org/10.1596/978-0-8213-7887-8 (page 233).

Baross, John A. and Sarah E. Hoffman (1985). "Submarine hydrothermal vents and associated gradient environments as sites for the origin and evolution of life". In: *Origins of life and evolution of the biosphere* 15.4, pp. 327–345. DOI: 10.1007/BF01808177. URL: https://doi.org/10.1007/BF01808177 (page 8).

Barstow, J.K. and P.G.J. Irwin (2016). "Habitable worlds with JWST: transit spectroscopy of the TRAPPIST-1 system?" In: *Monthly Notices of the Royal Astronomical Society* 461.1, pp. L92–L96 (page 148).

Beichman, Charles et al. (2014). "Observations of Transiting Exoplanets with the James Webb Space Telescope (JWST)". In: *Publications of the Astronomical Society of the Pacific* 126.946, pp. 1134–1173. DOI: 10.1086/679566. URL: http://dx.doi.org/10.1086/679566 (page 146).

Belbruno, Edward et al. (2012). "Chaotic Exchange of Solid Material Between Planetary Systems: Implications for Lithopanspermia". In: *Astrobiology* 12.8, pp. 754–774. DOI: 10.1089/ast.2012.0825. URL: https://doi.org/10.1089/ast.2012.0825 (page 144).

"Evolution from Molecules to Men" (1983). In: ed. by D. S. Bendall. Cambridge University Press. Chap. Gene, organism, and environment (page 55).

Benton, MJ (1995). "Diversification and extinction in the history of life". In: *Science* 268.5207, p. 52. DOI: 10.1126/science.7701342. URL: http://science.sciencemag.org/content/268/5207/52.abstract (page 224).

Beschta, Robert L. and W. J. Ripple (2006). "River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA". In: *Earth Surface Processes and Landforms* 31.12, pp. 1525–1539. DOI: 10.1002/esp.1362. URL: https://doi.org/10.1002/esp.1362 (page 31).

Betts, Holly C. et al. (2018). "Integrated genomic and fossil evidence illuminates life's early evolution and eukaryote origin". In: *Nature Ecology & Evolution* 2.10, pp. 1556–1562. DOI: 10.1038/s41559-018-0644-x. URL: https://doi.org/10.1038/s41559-018-0644-x (page 9).

Betts, Richard A and Timothy M. Lenton (2007). "Second chances for lucky Gaia: A hypothesis of Sequential Selection". Hadley Centre technical note 77 (page 51).

Bobrovskiy, Ilya et al. (2018). "Ancient steroids establish the Ediacaran fossil Dickinsonia as one of the earliest animals". In: *Science* 361.6408, p. 1246. DOI: 10.1126/science.aat7228. URL: http://science.sciencemag.org/content/361/6408/1246.abstract (page 9).

Borucki, William J. et al. (2010). "Kepler Planet-Detection Mission: Introduction and First Results". In: *Science* 327.5968, p. 977. DOI: 10.1126/science.1185402. URL: http://science.sciencemag.org/content/327/5968/977.abstract (page 146).

Bosak, T. et al. (2011). "Agglutinated tests in post-Sturtian cap carbonates of Namibia and Mongolia". In: *Earth and Planetary Science Letters* 308.1-2, pp. 29–40 (page 19).

Boston, Penelope J. and Stephen H. Schneider (1993). *Scientists on Gaia*. MIT Press (page 157).

Bouchard, Frédéric (2014). "Ecosystem Evolution is About Variation and Persistence, not Populations and Reproduction". In: *Biological Theory* 9.4, pp. 382–391. DOI: 10.1007/s13752-014-0171-1. URL: https://doi.org/10.1007/s13752-014-0171-1 (page 123).

Bourrat, Pierrick (2014). "From survivors to replicators: evolution by natural selection revisited". In: *Biology & Philosophy* 29.4, pp. 517–538. DOI: 10.1007/s10539-013-9383-1. URL: https://doi.org/10.1007/s10539-013-9383-1 (page 123).

Bowring, Samuel A. and Ian S. Williams (1999). "Priscoan (4.00 – 4.03 Ga) orthogneisses from northwestern Canada". In: *Contributions to Mineralogy and Petrology* 134.1, pp. 3–16. DOI: 10.1007/s004100050465. URL: https://doi.org/10.1007/s004100050465 (page 6).

Bowring, Samuel A et al. (2007). "Geochronologic constraints on the chronostratigraphic framework of the Neoproterozoic Huqf Supergroup, Sultanate of Oman". In: *American Journal of Science* 307.10, pp. 1097–1145 (page 16).

Brady, Patrick V. and Susan A. Carroll (1994). "Direct effects of CO2 and temperature on silicate weathering: Possible implications for climate control". In: *Geochimica et Cosmochimica Acta* 58.7, pp. 1853–1856. DOI: https://doi.org/10.1016/0016-7037(94)90543-6. URL: http://www.sciencedirect.com/science/article/pii/0016703794905436 (page 12).

Brasier, Martin D. et al. (2002). "Questioning the evidence for Earth's oldest fossils". In: *Nature* 416, 76 EP –. URL: https://doi.org/10.1038/416076a (page 8).

Brocks, Jochen J. et al. (1999). "Archean Molecular Fossils and the Early Rise of Eukaryotes". In: *Science* 285.5430, p. 1033. URL: http://science.sciencemag.org/content/285/5430/1033.abstract (pages 13, 97).

Burrows, Adam S. (2014). "Highlights in the study of exoplanet atmospheres". In: *Nature* 513, 345 EP –. URL: https://doi.org/10.1038/nature13782 (page 146).

Caldeira, Ken and James F. Kasting (1992). "Susceptibility of the early Earth to irreversible glaciation caused by carbon dioxide clouds". In: *Nature* 359, 226 EP –. URL: http://dx.doi.org/10.1038/359226a0 (page 18).

Calver, Clive R et al. (2004). "U-Pb zircon age constraints on late Neoproterozoic glaciation in Tasmania". In: *Geology* 32.10, pp. 893–896 (page 16).

Campbell, Ian H. and Richard J. Squire (2010). "The mountains that triggered the Late Neoproterozoic increase in oxygen: The Second Great Oxidation Event". In: *Geochimica et Cosmochimica Acta* 74.15, pp. 4187–4206. DOI: https://doi.org/10.1016/j.gca.2010.04.064. URL: http://www.sciencedirect.com/science/article/pii/S0016703710002498 (page 15).

Canfield, D. E. (2005). "THE EARLY HISTORY OF ATMOSPHERIC OXYGEN: Homage to Robert M. Garrels". In: *Annual Review of Earth and Planetary Sciences* 33.1, pp. 1–36. DOI: 10.1146/annurev.earth.33.092203.122711. URL: https://doi.org/10.1146/annurev.earth.33.092203.122711 (page 13).

Canfield, Don E., Simon W. Poulton, and Guy M. Narbonne (2007). "Late-Neoproterozoic Deep-Ocean Oxygenation and the Rise of Animal Life".

In: *Science* 315.5808, p. 92. DOI: 10.1126/science.1135013. URL: http://science.sciencemag.org/content/315/5808/92.abstract (page 15).

Canup, Robin M. and Erik Asphaug (2001). "Origin of the Moon in a giant impact near the end of the Earth's formation". In: *Nature* 412, 708 EP –. URL: http://dx.doi.org/10.1038/35089010 (page 5).

Carr, Michael H. (1996). "Water erosion on Mars and its biologic implications". In: *Endeavour* 20.2, pp. 56–60. DOI: https://doi.org/10.1016/0160-9327(96)10013-2. URL: http://www.sciencedirect.com/science/article/pii/0160932796100132 (page 141).

Carr, Michael H. et al. (1998). "Evidence for a subsurface ocean on Europa". In: *Nature* 391, 363 EP –. URL: https://doi.org/10.1038/34857 (page 142).

Carter, Brandon (1974). *Large number of coincidences and the anthropic principle in cosmology*. Vol. 63. Cambridge University Press, pp. 291–298 (pages 28, 60).

— (1983). "The anthropic principle and its implications for biological evolution". In: *Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences* 310.1512, p. 347. URL: http://rsta.royalsocietypublishing.org/content/310/1512/347.abstract (pages 28, 60).

Cassan, A. et al. (2012). "One or more bound planets per Milky Way star from microlensing observations". In: *Nature* 481, 167 EP –. URL: https://doi.org/10.1038/nature10684 (page 148).

Cassen, P., S. J. Peale, and R. T. Reynolds (1980). "Tidal dissipation in Europa: A correction". In: *Geophysical Research Letters* 7.11, pp. 987–988. DOI: 10.1029/GL007i011p00987. URL: https://doi.org/10.1029/GL007i011p00987 (page 142).

Cassen, P., R. T. Reynolds, and S. J. Peale (1979). "Is there liquid water on Europa?" In: *Geophysical Research Letters* 6.9, pp. 731–734. DOI: 10.1029/GL006i009p00731. URL: https://doi.org/10.1029/GL006i009p00731 (page 142).

Catling, David C., Kevin J. Zahnle, and Christopher P. McKay (2001). "Biogenic Methane, Hydrogen Escape, and the Irreversible Oxidation of Early Earth". In: *Science* 293, pp. 839–843 (page 93).

Chapman, Clark R., Barbara A. Cohen, and David H. Grinspoon (2007). "What are the real constraints on the existence and magnitude of the late heavy bombardment?" In: *Icarus* 189.1, pp. 233–245. DOI: https://doi.

org/10.1016/j.icarus.2006.12.020. URL: http://www.sciencedirect.com/science/article/pii/S0019103507000255 (page 7).

Charbonneau, David et al. (2002). "Detection of an Extrasolar Planet Atmosphere". In: *The Astrophysical Journal* 568.1, pp. 377–384. DOI: 10.1086/338770. URL: http://dx.doi.org/10.1086/338770 (page 145).

Charbonneau, David et al. (2005). "Detection of Thermal Emission from an Extrasolar Planet". In: *The Astrophysical Journal* 626.1, pp. 523–529. DOI: 10.1086/429991. URL: http://dx.doi.org/10.1086/429991 (page 145).

Chopra, Aditya and Charles H. Lineweaver (2016). "The Case for a Gaian Bottleneck: The Biology of Habitability". In: *Astrobiology* 16.1, pp. 7–22 (pages 1, 124, 150, 151, 154, 156, 229, 232).

Christensen, Kim et al. (2002). "Tangled Nature: A Model of Evolutionary Ecology". In: *Journal of Theoretical Biology* 216.1, pp. 73–84. DOI: https://doi.org/10.1006/jtbi.2002.2530. URL: http://www.sciencedirect.com/science/article/pii/S0022519302925300 (pages 51, 57, 224).

Christner, B. C. et al. (2003). "Bacterial recovery from ancient glacial ice." In: *Environmental Microbiology* 5.5, pp. 433–436 (page 19).

Chyba, C. (2000a). "correction: Energy for microbial life on Europa". In: *Nature* 406, 368 EP –. URL: https://doi.org/10.1038/35019159 (page 142).

Chyba, Christopher F. (2000b). "Energy for microbial life on Europa". In: *Nature* 403, 381 EP –. URL: https://doi.org/10.1038/35000281 (page 142).

Chyba, Christopher F. and Cynthia B. Phillips (2001). "Possible ecosystems and the search for life on Europa". In: *Proceedings of the National Academy of Sciences* 98.3, p. 801. DOI: 10.1073/pnas.98.3.801. URL: http://www.pnas.org/content/98/3/801.abstract (page 142).

— (2002). "Europa as an Abode of Life". In: *Origins of life and evolution of the biosphere* 32.1, pp. 47–67. DOI: 10.1023/A:1013958519734. URL: https://doi.org/10.1023/A:1013958519734 (page 142).

Claeys, Philippe and Alessandro Morbidelli (2011). "Late Heavy Bombardment". In: *Encyclopedia of Astrobiology*. Ed. by Muriel Gargaud et al. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 909–912. ISBN: 978-3-642-11274-4. DOI: 10.1007/978-3-642-11274-4_869. URL: https://doi.org/10.1007/978-3-642-11274-4_869 (page 6).

Clarke, Andrew (2014). "The thermal limits to life on Earth". In: *International Journal of Astrobiology* 13.2, pp. 141–154. DOI: 10.1017/S1473550413000438 (page 191).

Clarke, Ellen (2010). "The Problem of Biological Individuality". In: *Biological Theory* 5.4, pp. 312–325 (page 30).

Clarke, John T., S. Wannawichian, and D. Strobel (2010). "HST UV Observations Of The Extended Atmosphere Of Titan". In: *AAS/Division for Planetary Sciences Meeting Abstracts #42* (page 142).

Clynes, Manfred (1969). "CYBERNETIC IMPLICATIONS OF REIN CONTROL IN PERCEPTUAL AND CONCEPTUAL ORGANIZATION". In: *Annals of the New York Academy of Sciences* 156.2, pp. 629–664. DOI: 10.1111/j.1749-6632.1969.tb14005.x. URL: http://dx.doi.org/10.1111/j.1749-6632.1969.tb14005.x (page 67).

Cockell, Charles S. (2007). "Complete Course in Astrobiology". In: ed. by Horneck Gerda and Petra Rettberg. Wiley-Vch. Chap. Habitability, pp. 151 –177 (page 156).

Cockell, Charles S. et al. (2012). "Uninhabited habitats on Mars". In: *Icarus* 217.1, pp. 184–193. DOI: https://doi.org/10.1016/j.icarus.2011.10.025. URL: http://www.sciencedirect.com/science/article/pii/S0019103511004180 (page 189).

Collen, P. and R. J. Gibson (2000). "The general ecology of beavers (Castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish –a review". In: *Reviews in Fish Biology and Fisheries* 10.4, pp. 439–461. DOI: 10.1023/A:1012262217012. URL: https://doi.org/10.1023/A:1012262217012 (page 31).

Condon, Daniel et al. (2005). "U-Pb ages from the neoproterozoic Doushantuo Formation, China". In: *science* 308.5718, pp. 95–98 (page 16).

Cooley, Jeffrey L. (2008). "INANA AND ŠUKALETUDA: A SUMERIAN ASTRAL MYTH". In: *KASKAL Rivista di storia, ambienti e culture del Vicino Oriente Antico* 5 (page 138).

Copley, Shelley D., Eric Smith, and Harold J. Morowitz (2007). "The origin of the RNA world: Co-evolution of genes and metabolism". In: *Bioorganic Chemistry* 35.6, pp. 430–443. DOI: https://doi.org/10.1016/j.bioorg.2007.08.001. URL: http://www.sciencedirect.com/science/article/pii/S004520680700051X (page 8).

Craddock, Robert A. and Alan D. Howard (2002). "The case for rainfall on a warm, wet early Mars". In: *Journal of Geophysical Research: Planets* 107.E11, pp. 21–1–21–36. DOI: 10.1029/2001JE001505. URL: http://dx.doi.org/10.1029/2001JE001505 (page 189).

Crick, F. H. C. (1968). "The origin of the genetic code". In: *Journal of Molecular Biology* 38.3, pp. 367–379. DOI: https://doi.org/10.1016/0022-2836(68)90392-6. URL: http://www.sciencedirect.com/science/article/pii/0022283668903926 (page 8).

Crutzen, Paul J. (2006). "The "anthropocene"". In: *Earth system science in the anthropocene*. Springer, pp. 13–18 (page 20).

Dalrymple, G. Brent (2001). "The age of the Earth in the twentieth century: a problem (mostly) solved". In: *Geological Society, London, Special Publications* 190.1, p. 205. URL: http://sp.lyellcollection.org/content/190/1/205.abstract (page 5).

Danovaro, Roberto et al. (2010). "The first metazoa living in permanently anoxic conditions". In: *BMC Biology* 8.1, p. 30. DOI: 10.1186/1741-7007-8-30. URL: https://doi.org/10.1186/1741-7007-8-30 (pages 15, 16).

Darwin, Charles (1859). "On the Origin of Species by Means of Natural Selection, or, The Preservation of Favoured Races in the Struggle for Life". In: J. Murray. Chap. 14 (page 8).

Davies, P. C. W. (2004). "Does Life's Rapid Appearance Imply a Martian Origin?" In: *Astrobiology* 3.4, pp. 673–679. URL: https://doi.org/10.1089/153110703322736006 (page 230).

Davis, W.L. and C.P McKay (1996). "Origins of life: A comparison of theories and application to Mars". In: *Origins of life and evolution of the biosphere* 26.1, pp. 61–73 (page 230).

Dawkins, Richard (1982). *The Extended Phenotype*. Oxford University Press (pages 26, 27, 42, 65, 68, 96, 108).

— (1986). *The blind watchmaker: Why the evidence of evolution reveals a universe without design*. WW Norton & Company. ISBN: 0393315703 (page 27).

De Byle, Norbert V. (1964). "Detection of Functional Intraclonal Aspen Root Connections by Tracers and Excavation". In: *Forest Science* 10.4, pp. 386–396. URL: http://dx.doi.org/10.1093/forestscience/10.4.386 (page 30).

De Gregorio, S., R. A. Pielke, and G. A. Dalu (1992). "Feedback between a simple biosystem and the temperature of the Earth". In: *Journal of Nonlinear Science* 2.3, pp. 263–292. DOI: 10.1007/BF01208926. URL: https://doi.org/10.1007/BF01208926 (pages 161, 197).

De Vos, Jurriaan M. et al. (2015). "Estimating the normal background rate of species extinction". In: *Conservation Biology* 29.2, pp. 452–462. DOI: 10.1111/cobi.12380. URL: https://doi.org/10.1111/cobi.12380 (page 233).

Dieser, M., J. R. Battista, and B.C. Christner B. C. (2013). "Double-strand DNA break repair at -15C". In: *Applied Environmental Microbiology* 79.24 (page 19).

Djokic, Tara et al. (2017). "Earliest signs of life on land preserved in ca. 3.5 Ga hot spring deposits". In: *Nature Communications* 8, 15263 EP –. URL: http://dx.doi.org/10.1038/ncomms15263 (page 8).

Dodd, Matthew S. et al. (2017). "Evidence for early life in Earth's oldest hydrothermal vent precipitates". In: *Nature* 543, 60 EP –. URL: http://dx.doi.org/10.1038/nature21377 (page 8).

Donahue, T. M. et al. (1982). "Venus was wet: a measurement of the ratio of D to H". In: *Science* 216, pp. 630–633 (pages 138, 139, 156, 189).

Donnadieu, Yannick et al. (2004). "A 'snowball Earth' climate triggered by continental break-up through changes in runoff". In: *Nature* 428.6980, pp. 303–306. URL: http://dx.doi.org/10.1038/nature02408 (page 17).

Doolittle, W. Ford (1981). "Is nature really motherly?" In: *Coevolution Quarterly* 29, pp. 58–63 (pages 26, 27, 65, 68, 108).

— (2014). "Natural selection through survival alone, and the possibility of Gaia". In: *Biology & Philosophy* 29.3, pp. 415–423. DOI: 10.1007/s10539-013-9384-0. URL: http://dx.doi.org/10.1007/s10539-013-9384-0 (pages 1, 2, 62, 107, 109, 110, 135).

Doolittle, W. Ford (2019). "Making Evolutionary Sense of Gaia". In: *Trends in Ecology & Evolution*. DOI: https://doi.org/10.1016/j.tree.2019.05.001. URL: http://www.sciencedirect.com/science/article/pii/S0169534719301417 (page 26).

Downing, K and P Zvirinsky (1999). "The simulated evolution of biochemical guilds: reconciling Gaia theory and natural selection". In: *Artificial Life* 5.4, pp. 291–318 (pages 46, 66, 69, 92, 158, 227).

Downing, Keith (2000). "Exploring Gaia theory: Artificial life on a planetary scale". In: *Artificial Life* 7, pp. 90–99 (page 46).

Dyke, James G. (2010). "The Daisystat: A model to explore multidimensional homeostasis". URL: http://eprints.soton.ac.uk/272879/ (pages 38, 43–45, 56, 57, 67, 69, 227).

Dyke, James G. and I.S. Weaver (2013). "The emergence of environmental homeostasis in complex ecosystems". In: *PLoS Computational Biology* 9.5 (pages 67, 158).

Elachi, C. et al. (2005). "Cassini Radar Views the Surface of Titan". In: *Science* 308.5724, p. 970. DOI: 10.1126/science.1109919. URL: http://science.sciencemag.org/content/308/5724/970.abstract (page 142).

Evans, James (1998). *The History and Practice of Ancient Astronomy*. Oxford University Press (page 138).

Feinberg, Martin (1987). "Chemical reaction network structure and the stability of complex isothermal reactors—I. The deficiency zero and deficiency one theorems". In: *Chemical Engineering Science* 42.10, pp. 2229–2268. DOI: http://dx.doi.org/10.1016/0009-2509(87)80099-4. URL: http://www.sciencedirect.com/science/article/pii/0009250987800994 (page 160).

Forterre, Patrick (1999). "Displacement of cellular proteins by functional analogues from plasmids or viruses could explain puzzling phylogenies of many DNA informational proteins". In: *Molecular Microbiology* 33.3, pp. 457–465. DOI: 10.1046/j.1365-2958.1999.01497.x. URL: https://doi.org/10.1046/j.1365-2958.1999.01497.x (page 30).

— (2002). "The origin of DNA genomes and DNA replication proteins". In: *Current Opinion in Microbiology* 5.5, pp. 525–532. DOI: https://doi.org/10.1016/S1369-5274(02)00360-0. URL: http://www.sciencedirect.com/science/article/pii/S1369527402003600 (page 30).

Frank, S. et al. (2001). "Planetary habitability: is Earth commonplace in the Milky Way?" In: *Naturwissenschaften* 88.10, pp. 416–426 (page 150).

Free, Andrew and Nicholas H. Barton (2007). "Do evolution and ecology need the Gaia hypothesis?" In: *Trends in Ecology & Evolution* 22.11, pp. 611–619. DOI: https://doi.org/10.1016/j.tree.2007.07.007. URL: http://www.sciencedirect.com/science/article/pii/S0169534707002674 (pages 29, 30).

Gardner, Jonathan P. et al. (2006). "The James Webb Space Telescope". In: *Space Science Reviews* 123.4, pp. 485–606. DOI: 10.1007/s11214-006-8315-7. URL: https://doi.org/10.1007/s11214-006-8315-7 (page 146).

Gebauer, S. et al. (2018). "Evolution of Earth-like Planetary Atmospheres around M Dwarf Stars: Assessing the Atmospheres and Biospheres with a Coupled Atmosphere Biogeochemical Model". In: *Astrobiology* 18.7, pp. 856–872. DOI: 10.1089/ast.2017.1723. URL: https://doi.org/10.1089/ast.2017.1723 (page 232).

Gillon, Michaël et al. (2016). "Temperate Earth-sized planets transiting a nearby ultracool dwarf star". In: *Nature* 533, 221 EP –. URL: https://doi.org/10.1038/nature17448 (page 148).

Gillon, Michaël et al. (2017). "Seven temperate terrestrial planets around the nearby ultracool dwarf star TRAPPIST-1". In: *Nature* 542, 456 EP –. URL: https://doi.org/10.1038/nature21360 (page 148).

Gogarten-Boekels, Maria, Elena Hilario, and J. Peter Gogarten (1995). "The effects of heavy meteorite bombardment on the early evolution —The

emergence of the three Domains of life". In: *Origins of Life and Evolution of the Biosphere* 25.1, pp. 251–264. DOI: 10.1007/BF01581588. URL: https://doi.org/10.1007/BF01581588 (page 9).

Goldblatt, Colin (2016). "The inhabitance paradox: How habitability and inhabitancy are inseparable". In: *arXiv preprint arXiv:1603.00950* (pages 215, 229).

Goldblatt, Colin, Timothy M. Lenton, and Andrew J. Watson (2006). "Bistability of atmospheric oxygen and the Great Oxidation". In: *Nature* 443.7112, pp. 683–686. URL: http://dx.doi.org/10.1038/nature05169 (page 13).

Gough, D. O. (1981). "Solar Interior Structure and Luminosity Variations". In: *Physics of Solar Variations*. Ed. by V. Domingo. Dordrecht: Springer Netherlands, pp. 21–34. ISBN: 978-94-010-9633-1 (page 10).

Group, BABEL Working (1990). "Evidence for early Proterozoic plate tectonics from seismic reflection profiles in the Baltic shield". In: *Nature* 348, 34 EP –. URL: http://dx.doi.org/10.1038/348034a0 (page 7).

Haines, A et al. (2006). "Climate change and human health: impacts, vulnerability, and mitigation". In: *The Lancet* 367.9528, pp. 2101–2109. DOI: https://doi.org/10.1016/S0140-6736(06)68933-2. URL: http://www.sciencedirect.com/science/article/pii/S0140673606689332 (page 233).

Halliday, Alex N. (2000). "Terrestrial accretion rates and the origin of the Moon". In: *Earth and Planetary Science Letters* 176.1, pp. 17–30. DOI: https://doi.org/10.1016/S0012-821X(99)00317-9. URL: http://www.sciencedirect.com/science/article/pii/S0012821X99003179 (page 5).

Hamilton, W. D. (1964). "The genetical evolution of social behaviour". In: *Journal of Theoretical Biology* 7, pp. 17–52 (page 27).

— (1995). "Ecology in the Large: Gaia and Genghis Khan". In: *Journal of Applied Ecology* 32.3, pp. 451–453 (page 93).

Hansen, Candice J. et al. (2006). "Enceladus' Water Vapor Plume". In: *Science* 311.5766, p. 1422. DOI: 10.1126/science.1121254. URL: http://science.sciencemag.org/content/311/5766/1422.abstract (page 143).

Harland, WB (1964). "Critical evidence for a great infra-Cambrian glaciation". In: *Geologische Rundschau* 54.1 (page 16).

Hart, Michael H. (1979). "Habitable zones about main sequence stars". In: *Icarus* 37.1, pp. 351–357. DOI: https://doi.org/10.1016/0019-1035(79)90141-6. URL: http://www.sciencedirect.com/science/article/pii/0019103579901416 (page 144).

Heckman, Daniel S. et al. (2001). "Molecular Evidence for the Early Colonization of Land by Fungi and Plants". In: *Science* 293.5532, pp. 1129–1133. URL: http://science.sciencemag.org/content/293/5532/1129.abstract (page 17).

Heldmann, Jennifer L. et al. (2005). "Formation of Martian gullies by the action of liquid water flowing under current Martian environmental conditions". In: *Journal of Geophysical Research: Planets* 110.E5, n/a–n/a. DOI: 10.1029/2004JE002261. URL: http://dx.doi.org/10.1029/2004JE002261 (page 141).

Hessler, Angela M. et al. (2004). "A lower limit for atmospheric carbon dioxide levels 3.2 billion years ago". In: *Nature* 428, 736 EP –. URL: https://doi.org/10.1038/nature02471 (page 11).

Hoffman, P. F. (2013). "The Great Oxidation and a Siderian snowball Earth: MIF-S based correlation of Paleoproterozoic glacial epochs". In: *Chemical Geology* 362, pp. 143–156 (page 188).

Hoffman, P. F. et al. (1998). "A Neoproterozoic Snowball Earth". In: *Science* 281.5381, pp. 1342–1346 (pages 16, 18).

Hoffman, Paul F. (1999). "The break-up of Rodinia, birth of Gondwana, true polar wander and the snowball Earth". In: *Journal of African Earth Sciences* 28.1, pp. 17–33. DOI: https://doi.org/10.1016/S0899-5362(99)00018-4. URL: http://www.sciencedirect.com/science/article/pii/S0899536299000184 (page 17).

Hoffmann, K-H et al. (2004). "U-Pb zircon date from the Neoproterozoic Ghaub Formation, Namibia: constraints on Marinoan glaciation". In: *Geology* 32.9, pp. 817–820 (page 16).

Høgslund, Signe and Peter Bondo Christensen (2015). *Underwater drones map ice algae in Antarctica*. https://phys.org/news/2015-01-underwater-drones-ice-algae-antarctica.html (page 19).

Holland, Heinrich D. (1984). *The chemical evolution of the atmosphere and oceans*. Princeton University Press (page 26).

Höning, Dennis et al. (2014). "Biotic vs. abiotic Earth: A model for mantle hydration and continental coverage". In: *Planetary and Space Science* 98, pp. 5–13. DOI: https://doi.org/10.1016/j.pss.2013.10.004. URL: http://www.sciencedirect.com/science/article/pii/S0032063313002663 (pages 25, 32, 151).

Hood, L. L. et al. (2003). "Distribution of crustal magnetic fields on Mars: Shock effects of basin-forming impacts". In: *Geophysical Research Letters*

30.6. DOI: 10.1029/2002GL016657. URL: http://dx.doi.org/10.1029/2002GL016657 (page 140).

Hopkins, Michelle, T. Mark Harrison, and Craig E. Manning (2008). "Low heat flow inferred from >4 Gyr zircons suggests Hadean plate boundary interactions". In: *Nature* 456, 493 EP –. URL: http://dx.doi.org/10.1038/nature07465 (page 7).

Horneck, Gerda, David M. Klaus, and Rocco L. Mancinelli (2010). "Space Microbiology". In: *Microbiology and Molecular Biology Reviews* 74.1, p. 121. DOI: 10.1128/MMBR.00016-09. URL: http://mmbr.asm.org/content/74/1/121.abstract (page 143).

Hunten, D. M. and T. M. Donahue (1976). "Hydrogen loss from the terrestrial planets". In: *Annual Reviews of Earth and Planetary Sciences* 4.265 (page 13).

Iess, L. et al. (2014). "The Gravity Field and Interior Structure of Enceladus". In: *Science* 344.6179, p. 78. DOI: 10.1126/science.1250551. URL: http://science.sciencemag.org/content/344/6179/78.abstract (page 143).

Jakosky, Bruce M. et al. (1994). "Mars Atmospheric Loss and Isotopic Fractionation by Solar-Wind-Induced Sputtering and Photochemical Escape". In: *Icarus* 111.2, pp. 271–288. DOI: https://doi.org/10.1006/icar.1994.1145. URL: http://www.sciencedirect.com/science/article/pii/S0019103584711456 (page 141).

Jalasvuori, Matti and Bamford. Jaana K. H. (2008). "Structural Co-Evolution of Viruses and Cells in the Primordial World". In: *Origins of Life and Evolution of Biospheres* 38.2, pp. 165–181 (page 30).

Janssen, Annette B.G. et al. (2014). "Alternative stable states in large shallow lakes?" In: *Journal of Great Lakes Research* 40, pp. 813–826 (page 95).

Jessberger, EK et al. (1974). "High resolution argon analysis of neutron-irradiated Apollo 16 rocks and separated minerals". In: *Lunar and Planetary Science Conference Proceedings*. Ed. by Inc. New York Pergamon Press. Vol. 5, pp. 1419–1449 (page 6).

Jones, A. P. and K. T. Pickering (2003). "Evidence for aqueous fluid - sediment transport and erosional processes on Venus". In: *Journal of Geological Society* 160, pp. 319–327 (pages 139, 156, 189).

Jones, Clive G., John H. Lawton, and Moshe Shachak (1994). "Organisms as ecosystem engineers". In: *Oikos* 69.3, pp. 373–386 (page 94).

Kaltenegger, L. and D. Sasselov (2011). "Exploring the Habitable Zone for Kepler Planetary Candidates". In: *The Astrophysical Journal Letters* 736.2, p. L25. URL: http://stacks.iop.org/2041-8205/736/i=2/a=L25 (page 160).

Kamminga, Harmke (1982). "Life from space —A history of panspermia". In: *Vistas in Astronomy* 26, pp. 67–86. DOI: https://doi.org/10.1016/0083-6656(82)90001-0. URL: http://www.sciencedirect.com/science/article/pii/0083665682900010 (page 143).

Kasting, J. F. (1988). "Runaway and moist greenhouse atmospheres and the evolution of earth and Venus". In: *Icarus* 74, pp. 472–494 (pages 139, 156).

Kasting, J. F. and James C. G. Walker (1981). "Limits on oxygen concentration in the prebiological atmosphere and the rate of abiotic fixation of nitrogen". In: *Journal of Geophysical Research: Oceans* 86.C2, pp. 1147–1158. DOI: 10.1029/JC086iC02p01147. URL: https://doi.org/10.1029/JC086iC02p01147 (page 14).

Kasting, James F and Shuhei Ono (2006). "Palaeoclimates: the first two billion years". In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 361.1470, p. 917. URL: http://rstb.royalsocietypublishing.org/content/361/1470/917.abstract (page 13).

Kasting, James F., Daniel P. Whitmire, and Ray T. Reynolds (1993). "Habitable Zones around Main Sequence Stars". In: *Icarus* 101.1, pp. 108–128. DOI: https://doi.org/10.1006/icar.1993.1010. URL: http://www.sciencedirect.com/science/article/pii/S0019103583710109 (page 149).

Kasting, James F. et al. (2014). "Remote life-detection criteria, habitable zone boundaries, and the frequency of Earth-like planets around M and late K stars". In: *Proceedings of the National Academy of Sciences* 111.35, p. 12641. DOI: 10.1073/pnas.1309107110. URL: http://www.pnas.org/content/111/35/12641.abstract (page 149).

Kharecha, P., J Kasting, and J Siefert (2005). "A coupled atmosphere–ecosystem model of the early Archean Earth". In: *Geobiology* 3, pp. 53–76 (page 232).

Kirchner, James W. (1989). "The Gaia hypothesis: Can it be tested?" In: *Reviews of Geophysics* 27.2, pp. 223–235. DOI: 10.1029/RG027i002p00223. URL: https://doi.org/10.1029/RG027i002p00223 (pages 28, 226).

Kirschvink, J. L. (1992). "Late Proterozoic Low-Latitude Global Glaciation: The Snowball Earth". In: *The Proterozoic biosphere: a multidisciplinary study*. Ed. by J. W. Schopf and C. Klein. Cambridge Univ. Press (page 16).

Kite, Edwin S. and Eric B. Ford (2018). "Habitability of Exoplanet Waterworlds". In: *The Astrophysical Journal* 864.1, p. 75. DOI: 10.3847/1538-4357/aad6e0. URL: http://dx.doi.org/10.3847/1538-4357/aad6e0 (page 228).

Koch, David G. et al. (2010). "Kepler Mission Design, Realised Photometric Performance, and early Science". In: *The Astrophysical Journal* 713.2, pp. L79–L86. DOI: 10.1088/2041-8205/713/2/l79. URL: http://dx.doi.org/10.1088/2041-8205/713/2/L79 (page 146).

Kopp, Robert E. et al. (2005). "The Paleoproterozoic snowball Earth: A climate disaster triggered by the evolution of oxygenic photosynthesis". In: *Proceedings of the National Academy of Sciences* 102.32 (page 13).

Kopparapu, Ravi Kumar et al. (2013). "Habitable Zones around Main-sequence Stars: New Estimates". In: *The Astrophysical Journal* 765.2, p. 131. URL: http://stacks.iop.org/0004-637X/765/i=2/a=131 (pages 145, 148, 156, 157, 160, 189).

Kroll, John (2017). "Fire, ice, water, and dirt: A simple climate model". In: *Chaos: An Interdisciplinary Journal of Nonlinear Science* 27.7, p. 073101. DOI: 10.1063/1.4991383. URL: https://doi.org/10.1063/1.4991383 (page 232).

Kroneck, Peter MH and Martha E Sosa Torres (2015). *Sustaining life on planet earth: Metalloenzymes mastering dioxygen and other chewy gases*. Springer (page 146).

Kump, Lee R. (2008). "The rise of atmospheric oxygen". In: *Nature* 451, 277 EP –. URL: http://dx.doi.org/10.1038/nature06587 (pages 13, 15).

Kump, Lee R. and David Pollard (2008). "Amplification of Cretaceous Warmth by Biological Cloud Feedbacks". In: *Science* 320.5873, p. 195. URL: http://science.sciencemag.org/content/320/5873/195.abstract (page 12).

Laird, Simon and Henrik Jeldtoft Jensen (2006). "The Tangled Nature model with inheritance and constraint: Evolutionary ecology restricted by a conserved resource". In: *Ecological Complexity* 3.3, pp. 253–262. DOI: https://doi.org/10.1016/j.ecocom.2006.06.001. URL: http://www.sciencedirect.com/science/article/pii/S1476945X06000468 (pages 51, 57).

— (2007). "Correlation, selection and the evolution of species networks". In: *Ecological Modelling* 209.2, pp. 149–156. DOI: https://doi.org/10.1016/j.ecolmodel.2007.06.016. URL: http://www.sciencedirect.com/science/article/pii/S0304380007003249 (pages 51, 57).

Lan, Zhongwu et al. (2014). "A rapid and synchronous initiation of the wide spread Cryogenian glaciations". In: *Precambrian Research* 255, pp. 401–411. DOI: https://doi.org/10.1016/j.precamres.2014.10.015. URL: http:

//www.sciencedirect.com/science/article/pii/S0301926814003702 (page 16).

Lansing, J. S., J. N. Kremer, and B. B. Smuts (1998). "System-dependent selection, ecological feedback and the emergence of functional structure in ecosystems". In: *Journal of Theoretical Biology* 192, pp. 377–391 (page 42).

Lawson, Daniel, Henrik Jeldtoft Jensen, and Kunihiko Kaneko (2006). "Diversity as a product of inter-specific interactions". In: *Journal of Theoretical Biology* 243.3, pp. 299–307. DOI: https://doi.org/10.1016/j.jtbi.2006.07.007. URL: http://www.sciencedirect.com/science/article/pii/S0022519306002992 (pages 51, 57).

Le Hir, Guillaume et al. (2010). "Toward the snowball earth deglaciation..." In: *Climate Dynamics* 35.2, pp. 285–297. DOI: 10.1007/s00382-010-0748-8. URL: https://doi.org/10.1007/s00382-010-0748-8 (page 18).

Leconte, J. et al. (2013). "3D climate modeling of close-in land planets: Circulation patterns, climate moist bistability, and habitability". In: *Astronomy & Astrophysics* 554. URL: https://doi.org/10.1051/0004-6361/201321042 (page 148).

Lenardic, A., J.W. Crowley, and M. Weller (2016). "The Solar System of Forking Paths: Bifurcations in Planetary Evolution and the Search for Life-Bearing Planets in Our Galaxy". In: *Astrobiology* 16.7, pp. 551–559 (pages 151, 156, 188, 190).

Lenardic, Adrian and Johnny Seales (2019). "Different is More: The Value of Finding an Inhabited Planet that is Far From Earth 2.0". In: *Astrobiology* (page 228).

Lenton, T. M., H. J. Schellnhuber, and E. Szathmáry (2004). "Climbing the co-evolution ladder". In: *Nature* 431, 913 EP –. URL: https://doi.org/10.1038/431913a (page 29).

Lenton, Timothy M. (1998). "Gaia and natural selection". In: *Nature* 394.6692, pp. 439–447. URL: http://dx.doi.org/10.1038/28792 (pages 12, 24, 27, 65, 94, 109, 156, 173).

Lenton, Timothy M. (2001). "The role of land plants, phosphorus weathering and fire in the rise and regulation of atmospheric oxygen". In: *Global Change Biology* 7, pp. 613–629 (pages 96, 97).

Lenton, Timothy M (2004). "Scientists Debate Gaia". In: MIT Press Cambridge, MA. Chap. Clarifying Gaia: regulation with or without natural selection, pp. 15–25 (page 51).

Lenton, Timothy M., Ken Caldeira, and Eörs Szathmáry (2004). "Earth System Analysis for Sustainability". In: Dahlem Workshop Reports.

Chap. What does history teach us about the major transitions and role of disturbances in the evolution of life and of the earth system?, p. 29 (page 51).

Lenton, Timothy M. and Marcel van Oijen (2002). "Gaia as a complex adaptive system". In: *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 357.1421, p. 683. URL: http://rstb.royalsocietypublishing.org/content/357/1421/683.abstract (pages 25, 39, 40).

Lenton, Timothy M. and Andrew Watson (2011). *Revolutions that Made the Earth*. Oxford: OUP Oxford (pages 11–14, 17, 19).

Lenton, Timothy M. and David M. Wilkinson (2003). "Developing the Gaia Theory. A Response to the Criticisms of Kirchner and Volk". In: *Climatic Change* 58.1, pp. 1–12. ISSN: 1573-1480. DOI: 10.1023/A:1023498212441. URL: http://dx.doi.org/10.1023/A:1023498212441 (pages 29, 96, 226).

Lenton, Timothy M. et al. (2012). "First plants cooled the Ordovician". In: *Nature Geoscience* 5, 86 EP –. URL: http://dx.doi.org/10.1038/ngeo1390 (page 188).

Lenton, Timothy M. et al. (2016). "Earliest land plants created modern levels of atmospheric oxygen". In: *Proceedings of the National Academy of Sciences* 113.35, p. 9704. DOI: 10.1073/pnas.1604787113. URL: http://www.pnas.org/content/113/35/9704.abstract (page 15).

Lenton, Timothy M. et al. (2018). "Selection for Gaia across Multiple Scales". In: *Trends in Ecology & Evolution* 33.8, pp. 633–645. DOI: https://doi.org/10.1016/j.tree.2018.05.006. URL: http://www.sciencedirect.com/science/article/pii/S0169534718301186 (pages 57, 58, 109, 225).

Lewis, J. P., A. J. Weaver, and M. Eby (2007). "Snowball versus slushball Earth: Dynamic versus nondynamic sea ice?" In: *Journal of Geophysical Research: Oceans* 112.C11. DOI: 10.1029/2006JC004037. URL: https://doi.org/10.1029/2006JC004037 (page 20).

Lewis, Simon L. and Mark A. Maslin (2015). "Defining the Anthropocene". In: *Nature* 519, 171 EP –. URL: https://doi.org/10.1038/nature14258 (page 20).

Lofting, Hugh (1975). *Doctor Dolittle in the moon*. Penguin (page 26).

Lopes, Rosaly M. C. and Tracy K. P. Gregg (2004). *Volcanic Worlds: Exploring the Solar System's Volcanoes*. Springer Praxis Books (page 139).

Lovelock, James E. (1965). "A physical basis for life detection experiments". In: *Nature* 207.997, pp. 568–570 (pages 23, 141, 190).

Lovelock, James E. (1979). *Gaia, a new look at earth*. Oxford: Oxford University Press (pages 25, 108).

— (1988). *The ages of Gaia*. Oxford University Press (pages 12, 25).

— (1991). *Gaia The practical science of planetary medicine*. Oxford University Press (page 25).

— (1992). "A Numerical Model for Biodiversity". In: *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 338.1286, pp. 383–391. ISSN: 0962-8436. DOI: 10.1098/rstb.1992.0156. eprint: http://rstb.royalsocietypublishing.org/content/338/1286/383.full.pdf. URL: http://rstb.royalsocietypublishing.org/content/338/1286/383 (pages 42, 43).

— (2000). *The Ages of Gaia: A Biography of Our Living Earth, 2nd edition*. Oxford: OUP Oxford (pages 65, 156, 157).

— (2001). *Homage to Gaia: The life of an independent scientist*. Oxford University Press, USA (page 30).

— (2003). "Gaia and Emergence". In: *Climatic Change* 57.1, pp. 1–3 (pages 32, 223).

— (2007). *The revenge of gaia: earth's climate crisis & the fate of humanity*. Penguin. ISBN: 0465041698 (page 25).

— (2009). *A Final Warning: The Vanishing Face of Gaia*. Penguin London (page 25).

— (2015). *A rough ride to the future*. The Overlook Press (page 25).

Lovelock, James E. and Lynn Margulis (1974). "Atmospheric homeostasis by and for the biosphere: the Gaia hypothesis". In: *Tellus* 26, pp. 2–10 (pages 23, 25, 65, 156).

Lowe, Donald R. and Michael M. Tice (2004). "Geologic evidence for Archean atmospheric and climatic evolution: Fluctuating levels of CO2, CH4, and O2 with an overriding tectonic control". In: *Geology* 32.6, pp. 493–496. URL: http://dx.doi.org/10.1130/G20342.1 (page 11).

Lowell, Percival L. (1906). *Mars and Its Canals*. New York: Macmillan (page 140).

— (1908). *Mars as the Abode of Life*. New York: Macmillan (page 140).

Lunine, J.I. (2009). "Saturn's Titan: A strict test for life's cosmic ubiquity". In: *ArXiv e-prints* (page 143).

Lunine, Jonathan and Sushil Atreya (2008a). "The methane cycle on Titan". In: *Nature Geoscience* 1, 335 EP –. URL: https://doi.org/10.1038/ngeo187 (page 142).

Lunine, Jonathan I. and Sushil K. Atreya (2008b). "The methane cycle on Titan". In: *Nature Geoscience* 1, 159 EP –. URL: https://doi.org/10.1038/ngeo125 (page 142).

Macdonald, Francis A. et al. (2010). "Calibrating the Cryogenian". In: *Science* 327.5970, p. 1241. DOI: 10.1126/science.1183325. URL: http://science.sciencemag.org/content/327/5970/1241.abstract (page 16).

Margulis, Lynn and James E. Lovelock (1974). "Biological modulation of the Earth's atmosphere". In: *Icarus* 21.4, pp. 471–489. DOI: http://dx.doi.org/10.1016/0019-1035(74)90150-X. URL: http://www.sciencedirect.com/science/article/pii/001910357490150X (pages 23, 25, 108).

Marina 2 mission (1962). https://solarsystem.nasa.gov/missions/mariner02 (page 139).

McDonald-Gibson, J. et al. (2008). "Environmental regulation can arise under minimal assumptions". In: *Journal of Theoretical Biology* 251.4, pp. 653–666 (pages 56, 67, 69, 93, 158).

McKay, Christopher (2000). "Thickness of tropical ice and photosynthesis on a snowball earth". In: *Geophysical Research Letters* 27.14, pp. 2153–2156. DOI: 10.1029/2000GL008525. URL: https://doi.org/10.1029/2000GL008525 (page 19).

McKay, Christopher P. and Heather D. Smith (2005). "Possibilities for methanogenic life in liquid methane on the surface of Titan". In: *Icarus* 178.1, pp. 274–276 (page 142).

McKay, Christopher P. et al. (2014). "Follow the Plume: The habitability of Enceladus". In: *ASTROBIOLOGY* 14.4, pp. 352–355 (page 143).

McKee, Jeffrey K. et al. (2004). "Forecasting global biodiversity threats associated with human population growth". In: *Biological Conservation* 115.1, pp. 161–164. DOI: https://doi.org/10.1016/S0006-3207(03)00099-5. URL: http://www.sciencedirect.com/science/article/pii/S0006320703000995 (page 233).

Mendonça, Milton de Souza (2014). "Spatial ecology goes to space: Metabiospheres". In: *Icarus* 233, pp. 348–351. DOI: https://doi.org/10.1016/j.icarus.2014.01.027. URL: http://www.sciencedirect.com/science/article/pii/S001910351400058X (page 144).

Meyer, Cornelia et al. (2011). "Shock experiments in support of the Lithopanspermia theory: The influence of host rock composition, temperature, and shock pressure on the survival rate of endolithic and epilithic microorganisms". In: *Meteoritics & Planetary Science* 46.5, pp. 701–718. DOI: 10.1111/

j.1945-5100.2011.01184.x. URL: https://doi.org/10.1111/j.1945-5100.2011.01184.x (page 143).

Miller, Ron (2003). *Venus*. Twenty-First Century Books (page 138).

Milton, Daniel J. (1973). "Water and processes of degradation in the Martian landscape". In: *Journal of Geophysical Research* 78.20, pp. 4037–4047. DOI: 10.1029/JB078i020p04037. URL: http://dx.doi.org/10.1029/JB078i020p04037 (page 189).

Moore, CM et al. (2013). "Processes and patterns of oceanic nutrient limitation". In: *Nature geoscience* 6.9, p. 701 (page 212).

Moreira, David and Purificación López-García (2009). "Ten reasons to exclude viruses from the tree of life". In: *Nature Reviews Microbiology* 7, 306 EP –. URL: https://doi.org/10.1038/nrmicro2108 (page 30).

Nee, Sean (2004). "Extinction, Slime, and Bottoms". In: *PLOS Biology* 2.8, e272–. URL: https://doi.org/10.1371/journal.pbio.0020272 (page 188).

— (2007). *Metapopulations and their Spatial Dymanics (p 35-45) - Theoretical ecology; principles and applications.* 3rd. Oxford: Wiley-Blackwell (page 191).

Nesvorný, David, Fernando Roig, and William F. Bottke (2017). "Modeling the Historical Flux of Planetary Impactors". In: *The Astronomical Journal* 153.3, p. 103. URL: http://stacks.iop.org/1538-3881/153/i=3/a=103 (page 6).

Neveu, Marc, Hyo-Joong Kim, and Steven A. Benner (2013). "The "Strong" RNA World Hypothesis: Fifty Years Old". In: *Astrobiology* 13.4, pp. 391–403. DOI: 10.1089/ast.2012.0868. URL: https://doi.org/10.1089/ast.2012.0868 (page 8).

Newman, M. E. J. and Gunther J. Eble (1999). "Decline in extinction rates and scale invariance in the fossil record". In: *Paleobiology* 25.4, pp. 434–439. DOI: DOI:10.1017/S0094837300020303. URL: https://www.cambridge.org/core/article/decline-in-extinction-rates-and-scale-invariance-in-the-fossil-record/81A9096379FCD632352C34E8DFDB0054 (page 224).

Newman, M. E. J. and Paolo Sibani (1999). "Extinction, diversity and survivorship of taxa in the fossil record". In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266.1428, pp. 1593–1599. DOI: 10.1098/rspb.1999.0820. URL: https://doi.org/10.1098/rspb.1999.0820 (page 224).

Nicholson, Arwen E. et al. (2017). "Multiple states of environmental regulation in well-mixed model biospheres". In: *Journal of Theoretical Biology*

414, pp. 17–34. DOI: http://dx.doi.org/10.1016/j.jtbi.2016.11.019. URL: http://www.sciencedirect.com/science/article/pii/S0022519316303848 (pages 63, 110, 111, 113, 117, 125, 153, 158, 165, 173, 195).

Nicholson, Arwen E. et al. (2018). "Alternative mechanisms for Gaia". In: *Journal of Theoretical Biology* 457, pp. 249–257. DOI: https://doi.org/10.1016/j.jtbi.2018.08.032. URL: http://www.sciencedirect.com/science/article/pii/S0022519318304132 (page 107).

Nicholson, Arwen E et al. (2018). "Gaian bottlenecks and planetary habitability maintained by evolving model biospheres: the ExoGaia model". In: *Monthly Notices of the Royal Astronomical Society* 477.1, pp. 727–740. URL: http://dx.doi.org/10.1093/mnras/sty658 (page 154).

Nicholson, W. L. et al. (2000). "Resistance of Bacillus endospores to extreme terrestrial and exterterrestrial environments". In: *Microbiology and Molecular Biology Reviews* 64, pp. 548–572 (page 207).

Nicholson, Wayne L. (2009). "Ancient micronauts: interplanetary transport of microbes by cosmic impacts". In: *Trends in Microbiology* 17.6, pp. 243–250. DOI: https://doi.org/10.1016/j.tim.2009.03.004. URL: http://www.sciencedirect.com/science/article/pii/S0966842X09000900 (pages 143, 144).

Nisbet, E. G. and N. H. Sleep (2001). "The habitat and nature of early life". In: *Nature* 409.6823, pp. 1083–1091. URL: http://dx.doi.org/10.1038/35059210 (page 168).

Och, Lawrence M. and Graham A. Shields-Zhou (2012). "The Neoproterozoic oxygenation event: Environmental perturbations and biogeochemical cycling". In: *Earth-Science Reviews* 110.1, pp. 26–57. DOI: https://doi.org/10.1016/j.earscirev.2011.09.004. URL: http://www.sciencedirect.com/science/article/pii/S0012825211001498 (page 15).

Odling-Smee, F. John, Kevin N. Laland, and Marcus W. Feldman (1996). "Niche Construction". In: *The American Naturalist* 147.4, pp. 641–648. DOI: 10.1086/285870. URL: https://doi.org/10.1086/285870 (page 55).

Ojakangas, Gregory W. and David J. Stevenson (1989). "Thermal state of an ice shell on Europa". In: *Icarus* 81.2, pp. 220–241. DOI: https://doi.org/10.1016/0019-1035(89)90052-3. URL: http://www.sciencedirect.com/science/article/pii/0019103589900523 (page 142).

Ojha, Lujendra et al. (2015). "Spectral evidence for hydrated salts in recurring slope lineae on Mars". In: *Nature Geosci* 8.11, pp. 829–832. URL: http://dx.doi.org/10.1038/ngeo2546 (page 141).

O'Malley-James, J. T. et al. (2012). "Life and Light: Exotic Photosynthesis in Binary and Multiple-Star Systems". In: *Astrobiology* 12.2, pp. 115–124. DOI: 10.1089/ast.2011.0678. URL: https://doi.org/10.1089/ast.2011.0678 (page 146).

Own, Tobias, Robert D. Cess, and V. Ramanathan (1979). "Enhanced CO2 greenhouse to compensate for reduced solar luminosity on early Earth". In: *Nature* 277, 640 EP –. URL: https://doi.org/10.1038/277640a0 (page 11).

Paine, Robert T. (1969). "A Note on Trophic Complexity and Community Stability". In: *The American Naturalist* 103.929, pp. 91–93 (page 94).

Paolo, Ezequiel A. Di et al. (2000). *Simulation models as opaque thought experiments* (page 157).

Parkinson, Christopher D. et al. (2008). "Habitability of Enceladus: Planetary Conditions for Life". In: *Origins of Life and Evolution of Biospheres* 38.4, pp. 355–369. DOI: 10.1007/s11084-008-9135-4. URL: http://dx.doi.org/10.1007/s11084-008-9135-4 (page 143).

Patz, Jonathan A. et al. (2005). "Impact of regional climate change on human health". In: *Nature* 438, 310 EP –. URL: https://doi.org/10.1038/nature04188 (page 233).

Pavlov, A. A. et al. (2000). "Greenhouse warming by CH_4 in the atmosphere of early Earth". In: *Journal of Geophysical Research* 105.11981 (page 12).

Pearson, Helen (2008). "'Virophage' suggests viruses are alive". In: *Nature* 454.677 (page 30).

Pepin, Robert O. (1994). "Evolution of the Martian Atmosphere". In: *Icarus* 111.2, pp. 289–304. DOI: https://doi.org/10.1006/icar.1994.1146. URL: http://www.sciencedirect.com/science/article/pii/S0019103584711468 (page 189).

Perraudin, Frances (2019). *Extinction Rebellion arrests pass 1,000 on eighth day of protests*. The Guardian (page 233).

Petigura, Erik A, Andrew W Howard, and Geoffrey W Marcy (2013). "Prevalence of Earth-size planets orbiting Sun-like stars". In: *Proceedings of the National Academy of Sciences of the United States of America* 110.48, pp. 19273–19278. DOI: 10.1073/pnas.1319909110. URL: https://www.ncbi.nlm.nih.gov/pubmed/24191033 (page 148).

Phillips, Michael K., Douglas W. Smith, and Barry O'Neill (1996). *The wolves of Yellowstone*. Voyageur Press Stillwater, MN (page 31).

Pierrehumbert, R. T. (2005). "Climate dynamics of a hard snowball Earth". In: *Journal of Geophysical Research: Atmospheres* 110.D1. DOI: 10.1029/2004JD005162. URL: https://doi.org/10.1029/2004JD005162 (page 18).

Pierrehumbert, Raymond and Eric Gaidos (2011). "Hydrogen Greenhouse Planets Beyond The Habitable Zone". In: *The Astrophysical Journal* 734.1, p. L13. DOI: 10.1088/2041-8205/734/1/l13. URL: http://dx.doi.org/10.1088/2041-8205/734/1/L13 (pages 145, 149).

Pierrehumbert, Raymond T. (2004). "High levels of atmospheric carbon dioxide necessary for the termination of global glaciation". In: *Nature* 429, 646 EP –. URL: http://dx.doi.org/10.1038/nature02640 (page 18).

Pimm, Stuart L. and Peter Raven (2000). "Extinction by numbers". In: *Nature* 403, 843 EP –. URL: https://doi.org/10.1038/35002708 (page 233).

Podosek, Frank A. and Patrick Cassen (1994). "Theoretical, observational, and isotopic estimates of the lifetime of the solar nebula". In: *Meteoritics* 29.1, pp. 6–25. DOI: 10.1111/j.1945-5100.1994.tb00649.x. URL: https://doi.org/10.1111/j.1945-5100.1994.tb00649.x (page 5).

Pollack, J. B. et al. (1987). "The case for a wet, warm climate on early Mars". In: *Icarus* 71.2, pp. 203–224. DOI: http://dx.doi.org/10.1016/0019-1035(87)90147-3. URL: http://www.sciencedirect.com/science/article/pii/0019103587901473 (page 138).

Postberg, Frank et al. (2018). "Macromolecular organic compounds from the depths of Enceladus". In: *Nature* 558.7711, pp. 564–568. DOI: 10.1038/s41586-018-0246-4. URL: https://doi.org/10.1038/s41586-018-0246-4 (page 143).

Poulton, Simon W. and Donald E. Canfield (2011). "Ferruginous Conditions: A Dominant Feature of the Ocean through Earth's History". In: *Elements* 7.2, pp. 107–112 (page 7).

Prave, Anthony R et al. (2016). "Duration and nature of the end-Cryogenian (Marinoan) glaciation". In: *Geology* 44.8, pp. 631–634 (page 16).

Raup, D M and J W Valentine (1983). "Multiple origins of life". In: *Proceedings of the National Academy of Sciences* 80.10, p. 2981. URL: http://www.pnas.org/content/80/10/2981.abstract (page 8).

Raup, David M. and J. John Sepkoski (1982). "Mass Extinctions in the Marine Fossil Record". In: *Science* 215.4539, p. 1501. URL: http://science.sciencemag.org/content/215/4539/1501.abstract (page 188).

Rein, Hanno (2012). "A proposal for community driven and decentralized astronomical databases and the Open Exoplanet Catalogue". In: *arXiv preprint arXiv:1211.7121* (page 149).

Reyes-Ruiz, M. et al. (2012). "Dynamics of escaping Earth ejecta and their collision probabilities with different Solar System bodies". In: *Icarus* 220.2, pp. 777–786. DOI: https://doi.org/10.1016/j.icarus.2012.06.017. URL: http://www.sciencedirect.com/science/article/pii/S0019103512002461 (page 143).

Ribas, Ignasi (2009). "The Sun and stars as the primary energy input in planetary atmospheres". In: *Proceedings of the International Astronomical Union* 5.S264, pp. 3–18. DOI: DOI:10.1017/S1743921309992298 (pages 10, 11).

Ripple, William J. and Robert L. Beschta (2006). "Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem". In: *Forest Ecology and Management* 230.1, pp. 96–106. DOI: https://doi.org/10.1016/j.foreco.2006.04.023. URL: http://www.sciencedirect.com/science/article/pii/S0378112706002726 (page 31).

— (2007). "Restoring Yellowstone's aspen with wolves". In: *Biological Conservation* 138.3, pp. 514–519. DOI: https://doi.org/10.1016/j.biocon.2007.05.006. URL: http://www.sciencedirect.com/science/article/pii/S0006320707001966 (page 31).

Ripple, William J and Eric J Larsen (2000). "Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA". In: *Biological Conservation* 95.3, pp. 361–370. DOI: https://doi.org/10.1016/S0006-3207(00)00014-8. URL: http://www.sciencedirect.com/science/article/pii/S0006320700000148 (page 31).

Robertson, Michael P and Gerald F Joyce (2012). "The Origins of the RNA World". In: *Cold Spring Harbor Perspectives in Biology* 4.5, a003608. DOI: 10.1101/cshperspect.a003608. URL: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3331698/ (page 8).

Rooney, Alan D. et al. (2014). "Re-Os geochronology and coupled Os-Sr isotope constraints on the Sturtian snowball Earth". In: *Proceedings of the National Academy of Sciences* 111.1, p. 51. DOI: 10.1073/pnas.1317266110. URL: http://www.pnas.org/content/111/1/51.abstract (page 16).

Rooney, Alan D et al. (2015). "A Cryogenian chronology: Two long-lasting synchronous Neoproterozoic glaciations". In: *Geology* 43.5, pp. 459–462 (page 16).

Rosing, Minik T. et al. (2010). "No climate paradox under the faint early Sun". In: *Nature* 464.7289, pp. 744–747. URL: http://dx.doi.org/10.1038/nature08955 (page 12).

Ross, M. N. and G. Schubert (1987). "Tidal heating in an internal ocean model of Europa". In: *Nature* 325.6100, pp. 133–134. DOI: 10.1038/325133a0. URL: https://doi.org/10.1038/325133a0 (page 142).

Rye, R., P. H. Kuo, and H. D Holland (1995). "Atmospheric carbon dioxide concentrations before 2.2 billion years ago". In: *Nature* 387.603 (page 11).

Sagan, Carl and George Mullen (1972). "Earth and Mars: Evolution of atmospheres and surface temperatures". In: *Science* 177.4043, pp. 52–56 (page 11).

Sapp, Jan (2009). *The New Foundations of Evolution: On the Tree of Life*. Oxford University Press (page 166).

Saunders, Peter, Johan H. Koeslag, and Jabus A. Wessels (1998). "Integral Rein Control in Physiology". In: *Journal of theoretical biology* 194, pp. 163–73. DOI: 10.1006/jtbi.1998.0746 (pages 56, 226).

Saunders, Peter T. (1994). "Evolution without Natural Selection: Further Implications of the Daisyworld Parable". In: *Journal of Theoretical Biology* 166.4, pp. 365–373. DOI: https://doi.org/10.1006/jtbi.1994.1033. URL: http://www.sciencedirect.com/science/article/pii/S0022519384710332 (pages 161, 197).

Scheffer, M et al. (1993). "Alternative equilibria in shallow lakes." In: *Trends in Ecology and Evolution* 8, pp. 275–279 (page 95).

Schiaparelli, G. V. (1882). "On some observations of Saturn and Mars". In: *The Observatory* 5, pp. 221–224 (page 140).

Schneider, Stephen H. et al. (2013). *Scientists Debate Gaia: The Next Century*. MIT Press Scholarship Online (pages 23, 158).

Schneider, Stephen Henry and Randi Londer (1984). *Coevolution of climate and life*. Sierra Club Books (page 26).

Schopf, J. William et al. (2017). "SIMS analyses of the oldest known assemblage of microfossils document their taxon-correlated carbon isotope compositions". In: *Proceedings of the National Academy of Sciences*. URL: http://www.pnas.org/content/early/2017/12/12/1718063115.abstract (page 8).

Schrag, Daniel P. and Paul F. Hoffman (2001). "Geophysics: Life, geology and snowball Earth". In: *Nature* 409.6818, pp. 306–306. URL: http://dx.doi.org/10.1038/35053170 (page 16).

Schröder, K. P. and Robert Connon Smith (2008). "Distant future of the Sun and Earth revisited". In: *Monthly Notices of the Royal Astronomical Society* 386.1, pp. 155–163. URL: http://dx.doi.org/10.1111/j.1365-2966.2008.13022.x (page 10).

Schulze-Makuch, Dirk and Louis N. Irwin (2002). "Reassessing the Possibility of Life on Venus: Proposal for an Astrobiology Mission". In: *Astrobiology* 2.2, pp. 197–202. DOI: 10.1089/15311070260192264. URL: https://doi.org/10.1089/15311070260192264 (page 140).

Schwartzman, David W and Tyler Volk (1989). "Biotic enhancement of weathering and the habitability of Earth". In: *Nature* 340.6233, pp. 457–460 (page 25).

— (1991). "Biotic enhancement of weathering and surface temperatures on Earth since the origin of life". In: *Palaeogeography, Palaeoclimatology, Palaeoecology* 90.4, pp. 357–371 (page 25).

Seager, S., W. Bains, and J. J. Petkowski (2016). "Toward a List of Molecules as Potential Biosignature Gases for the Search for Life on Exoplanets and Applications to Terrestrial Biochemistry". In: *Astrobiology* 16.6, pp. 465–485. DOI: 10.1089/ast.2015.1404. URL: https://doi.org/10.1089/ast.2015.1404 (page 146).

Seager, Sara (2013). "Exoplanet Habitability". In: *Science* 340.6132, p. 577. DOI: 10.1126/science.1232226. URL: http://science.sciencemag.org/content/340/6132/577.abstract (page 149).

Seager, Sara (2014). "The future of spectroscopic life detection on exoplanets". In: *Proceedings of the National Academy of Sciences* 111.35, p. 12634. URL: http://www.pnas.org/content/111/35/12634.abstract (pages 146, 149).

Semenza, Gregg L. (2007). "Life with Oxygen". In: *Science* 318.5847, p. 62. DOI: 10.1126/science.1147949. URL: http://science.sciencemag.org/content/318/5847/62.abstract (page 9).

Service, National Park. *Wolves*. https://www.nps.gov/yell/learn/nature/wolves.htm (page 32).

Sheehan, William (1996). *The Planet Mars: A History of Observation & Discovery*. The University of Arizona Press (page 140).

Siebert, J. et al. (1996). "Cryptoendolithic microorganisms from Antarctic sandstone of Linnaeus Terrace (Asgard Range): diversity, properties and interactions". In: *Biodiversity and Conservation* 5, pp. 1337–1363 (pages 142, 191).

Sleep, Norman H. (2010). "The Hadean-Archaean Environment". In: *Cold Spring Harbor Perspectives in Biology*. URL: http://cshperspectives.cshlp.org/content/early/2010/04/30/cshperspect.a002527. (page 6).

Sleep, Norman H. and Brian F. Windley (1982). "Archean Plate Tectonics: Constraints and Inferences". In: *The Journal of Geology* 90.4, pp. 363–379. DOI: 10.1086/628691. URL: https://doi.org/10.1086/628691 (page 7).

Sleep, Norman H. and Kevin Zahnle (1998). "Refugia from asteroid impacts on early Mars and the early Earth". In: *Journal of Geophysical Research: Planets* 103.E12, pp. 28529–28544. DOI: 10.1029/98JE01809. URL: https://doi.org/10.1029/98JE01809 (page 144).

— (2001). "Carbon dioxide cycling and implications for climate on ancient Earth". In: *Journal of Geophysical Research: Planets* 106.E1, pp. 1373–1399. DOI: 10.1029/2000JE001247. URL: https://doi.org/10.1029/2000JE001247 (page 11).

Smith, Douglas W., Rolf O. Peterson, and Douglas B. Houston (2003). "Yellowstone after Wolves". In: *BioScience* 53.4, pp. 330–340. URL: http://dx.doi.org/10.1641/0006-3568(2003)053[0330:YAW]2.0.CO;2 (page 31).

Smith, M. Paul and David A. T. Harper (2013). "Causes of the Cambrian Explosion". In: *Science* 341.6152, p. 1355. DOI: 10.1126/science.1239450. URL: http://science.sciencemag.org/content/341/6152/1355.abstract (page 9).

Sober, E. (2008). "Evidence and Evolution". In: Cambridge University Press (page 8).

Sober, Elliott and Michael Steel (2002). "Testing the Hypothesis of Common Ancestry". In: *Journal of Theoretical Biology* 218.4, pp. 395–408. DOI: https://doi.org/10.1006/jtbi.2002.3086. URL: http://www.sciencedirect.com/science/article/pii/S0022519302930869 (page 8).

Soderblom, Laurence A. et al. (2007). "Topography and geomorphology of the Huygens landing site on Titan". In: *Planetary and Space Science* 55.13, pp. 2015–2024. DOI: https://doi.org/10.1016/j.pss.2007.04.015. URL: http://www.sciencedirect.com/science/article/pii/S0032063307001298 (page 142).

Solé, R. V. and A. Munteanu (2004). "The large-scale organization of chemical reaction networks in astrophysics". In: *EPL (Europhysics Letters)* 68.2, p. 170. URL: http://stacks.iop.org/0295-5075/68/i=2/a=170 (page 160).

Sorrell, Wilfred H. (2001). "Origin of Amino Acids and Organic Sugars in Interstellar Clouds". In: *The Astrophysical Journal Letters* 555.2, p. L129. URL: http://stacks.iop.org/1538-4357/555/i=2/a=L129 (page 148).

Spencer, J. R. et al. (2006). "Cassini Encounters Enceladus: Background and the Discovery of a South Polar Hot Spot". In: *Science* 311.5766, p. 1401.

DOI: 10.1126/science.1121661. URL: http://science.sciencemag.org/content/311/5766/1401.abstract (page 143).

Spencer, John R. et al. (2009). "Enceladus: An Active Cryovolcanic Satellite". In: *Saturn from Cassini-Huygens*. Ed. by Michele K. Dougherty, Larry W. Esposito, and Stamatios M. Krimigis. Dordrecht: Springer Netherlands, pp. 683–724. ISBN: 978-1-4020-9217-6. DOI: 10.1007/978-1-4020-9217-6{_}21. URL: http://dx.doi.org/10.1007/978-1-4020-9217-6_21 (page 143).

Spudis, Paul D., Don E. Wilhelms, and Mark S. Robinson (2011). "The Sculptured Hills of the Taurus Highlands: Implications for the relative age of Serenitatis, basin chronologies and the cratering history of the Moon". In: *Journal of Geophysical Research: Planets* 116.E12. DOI: 10.1029/2011JE003903. URL: https://doi.org/10.1029/2011JE003903 (page 7).

Squyres, S. W. et al. (2008). "Detection of Silica-Rich Deposits on Mars". In: *Science* 320.5879, p. 1063. DOI: 10.1126/science.1155429. URL: http://science.sciencemag.org/content/320/5879/1063.abstract (page 142).

Squyres, Steven W. and James F. Kasting (1994). "Early Mars: How Warm and How Wet?" In: *Science* 265.5173, p. 744. URL: http://science.sciencemag.org/content/265/5173/744.abstract (page 138).

Squyres, Steven W. et al. (1983). "Liquid water and active resurfacing on Europa". In: *Nature* 301.5897, pp. 225–226. DOI: 10.1038/301225a0. URL: https://doi.org/10.1038/301225a0 (page 142).

Stahler, Daniel R., Douglas W. Smith, and Debra S. Guernsey (2006). "Foraging and Feeding Ecology of the Gray Wolf (Canis lupus): Lessons from Yellowstone National Park, Wyoming, USA". In: *The Journal of Nutrition* 136.7, 1923S–1926S. URL: http://dx.doi.org/10.1093/jn/136.7.1923S (page 31).

Stevenson, David J (1983). "The nature of the earth prior to the oldest known rock record-The Hadean earth". In: *IN: Earth's earliest biosphere: Its origin and evolution (A84-43051 21-51). Princeton, NJ, Princeton University Press, 1983, p. 32-40.* Pp. 32–40 (page 6).

Stix, Michael (2002). *The Sun*. Springer-Verlag Berlin Heidelberg (page 10).

Suttle, Curtis A. (2007). "Marine viruses - major players in the global ecosystem". In: *Nature Reviews Microbiology* 5, 801 EP –. URL: https://doi.org/10.1038/nrmicro1750 (page 30).

Svedhem, Hakan et al. (2007). "Venus as a more Earth-like planet". In: *Nature* 450.7170, pp. 629–632. URL: http://dx.doi.org/10.1038/nature06432 (page 139).

Szathmáry, Eörs and John Maynard Smith (1995). *The major transitions in evolution*. WH Freeman Spektrum (page 26).

Tang, Haoshu and Yanjing Chen (2013). "Global glaciations and atmospheric change at ca. 2.3 Ga". In: *Geoscience Frontiers* 4.5, pp. 583–596. DOI: https://doi.org/10.1016/j.gsf.2013.02.003. URL: http://www.sciencedirect.com/science/article/pii/S1674987113000297 (page 17).

Tera, F., D. A. Papanastassiou, and G. J. Wasserburg (1973). "A lunar cataclysm at ~3.95 AE and the structure of the lunar crust". In: 4, pp. 723–725 (page 6).

Tera, Fouad, D. A. Papanastassiou, and G. J. Wasserburg (1974). "Isotopic evidence for a terminal lunar cataclysm". In: *Earth and Planetary Science Letters* 22.1, pp. 1–21. DOI: https://doi.org/10.1016/0012-821X(74)90059-4. URL: http://www.sciencedirect.com/science/article/pii/0012821X74900594 (page 6).

Theobald, Douglas L. (2010). "A formal test of the theory of universal common ancestry". In: *Nature* 465, 219 EP –. URL: http://dx.doi.org/10.1038/nature09014 (page 8).

Tian, Feng et al. (2005). "A Hydrogen-Rich Early Earth Atmosphere". In: *Science* 308.5724, p. 1014. URL: http://science.sciencemag.org/content/308/5724/1014.abstract (page 7).

Tilman, David (1980). "Resources: A Graphical-Mechanistic Approach to Competition and Predation". In: *The American Naturalist* 116.3, pp. 362–393 (page 73).

Toman, Jan and Jaroslav Flegr (2017). "Stability-based sorting: The forgotten process behind (not only) biological evolution". In: *Journal of Theoretical Biology* 435, pp. 29–41 (page 109).

Turner, G and P Cadogan (1975). "The history of lunar bombardment inferred from ^{40}Ar-^{39}Ar dating". In: *Proceedings of the Lunar Science Conference*. Vol. 6, pp. 1509–1538 (page 6).

Tyrrell, Toby (2004). "Biotic plunder: control of the environment by biological exhaustion of resources". In: *Schneider, S.H., Miller, J.R., Crist, E. and Boston, P.J. (eds.) Scientists debate Gaia: the next Century. Cambridge MA, USA, MIT Press*, pp. 137–147 (pages 30, 73, 211).

Tziperman, Eli et al. (2011). "Biologically induced initiation of Neoproterozoic snowball-Earth events". In: *Proceedings of the National Academy of Sciences* 108.37, p. 15091. DOI: 10.1073/pnas.1016361108. URL: http://www.pnas.org/content/108/37/15091.abstract (page 17).

Udry, Stéphane and Nuno C. Santos (2007). "Statistical Properties of Exoplanets". In: *Annual Review of Astronomy and Astrophysics* 45.1, pp. 397–439. DOI: 10.1146/annurev.astro.45.051806.110529. URL: https://doi.org/10.1146/annurev.astro.45.051806.110529 (page 146).

Vago, Jorge L. et al. (2017). "Habitability on Early Mars and the Search for Biosignatures with the ExoMars Rover". In: *Astrobiology* 17.6-7, pp. 471–510. URL: https://doi.org/10.1089/ast.2016.1533 (page 142).

Valley, John W. et al. (2002). "A cool early Earth". In: *Geological Society of America* 30.4, pp. 351–354 (pages 6, 11).

Valtonen, Mauri et al. (2008). "Natural transfer of viable microbes in space from planets in extra-solar systems to a planet in our solar system and vice versa". In: *The Astrophysical Journal* 690.1, pp. 210–215. DOI: 10.1088/0004-637x/690/1/210. URL: http://dx.doi.org/10.1088/0004-637X/690/1/210 (page 144).

Venera 7 mission (1970). https://solarsystem.nasa.gov/missions/Venera_07 (page 139).

Villarreal, Luis P. and Victor R. DeFilippis (2000). "A Hypothesis for DNA Viruses as the Origin of Eukaryotic Replication Proteins". In: *Journal of Virology* 74.15, p. 7079. DOI: 10.1128/JVI.74.15.7079-7084.2000. URL: http://jvi.asm.org/content/74/15/7079.abstract (page 30).

Volk, Tyler (1998). *Gaia's Body: Towards a Physiology of Earth*. Springer New York (pages 27, 92, 109).

Von Bloh, W, Arthur Block, and Hans-Joachim Schellnhuber (1997). "Self-stabilization of the biosphere under global change: a tutorial geophysiological approach". In: *Tellus B* 49.3, pp. 249–262 (pages 39–41).

Walker, James C. G. and Peter Brimblecombe (1985). "Iron and sulfur in the pre-biologic ocean". In: *Precambrian Research* 28.3, pp. 205–222. DOI: https://doi.org/10.1016/0301-9268(85)90031-2. URL: http://www.sciencedirect.com/science/article/pii/0301926885900312 (page 7).

Walker, James C. G., P. B. Hays, and J. F. Kasting (1981). "A negative feedback mechanism for the long-term stabilization of Earth's surface temperature". In: *Journal of Geophysical Research: Oceans* 86.C10, pp. 9776–9782. DOI: 10.1029/JC086iC10p09776. URL: https://doi.org/10.1029/JC086iC10p09776 (page 11).

Walker, Marilyn D. et al. (2006). "Plant community responses to experimental warming across the tundra biome". In: *Proceedings of the National Academy of Sciences* 103.5, pp. 1342–1346 (page 95).

Wang, Rong et al. (2012). "Flickering gives early warning signals of a critical transition to a eutrophic lake state". In: *Nature* 492.7429, pp. 419–422. URL: http://dx.doi.org/10.1038/nature11655 (page 93).

Watson, Andrew J (2004). "Gaia and observer self-selection". In: *Scientists Debate Gaia*, pp. 201–208 (pages 29, 60, 226).

Watson, Andrew J. and James E. Lovelock (1983). "Biological homeostasis of the global environment: the parable of Daisyworld". In: *Tellus* 35B, pp. 284–289 (pages 25, 26, 35, 39, 65, 69, 92, 157, 161, 165, 197, 221).

Watters, Thomas R. and Richard A. Schultz, eds. (2010). *Planetary Tectonics*. Cambridge University Press (page 141).

Way, M. J. et al. (2016). "Was Venus the first habitable world of our solar system?" In: *Geophysical Research Letters* 43.16, pp. 8376–8383. DOI: 10.1002/2016GL069790. URL: http://dx.doi.org/10.1002/2016GL069790 (pages 138, 157).

Weber, S. L. (2001). "On Homeostasis in Daisyworld". In: *Climatic Change* 48.2, pp. 465–485. DOI: 10.1023/A:1010774325080. URL: https://doi.org/10.1023/A:1010774325080 (pages 161, 197).

Weller, M. B., A. Lenardic, and C. O'Neill (2015). "The effects of internal heating and large scale climate variations on tectonic bi-stability in terrestrial planets". In: *Earth and Planetary Science Letters* 420, pp. 85–94. DOI: https://doi.org/10.1016/j.epsl.2015.03.021. URL: http://www.sciencedirect.com/science/article/pii/S0012821X15001648 (page 151).

Weller, Matthew B. and Adrian Lenardic (2018). "On the evolution of terrestrial planets: Bi-stability, stochastic effects, and the non-uniqueness of tectonic states". In: *Geoscience Frontiers* 9.1, pp. 91–102. DOI: https://doi.org/10.1016/j.gsf.2017.03.001. URL: http://www.sciencedirect.com/science/article/pii/S1674987117300488 (page 151).

Wells, L. E., J. C. Armstrong, and G. Gonzalez (2003). "Reseeding of early Earth by impacts of returning ejecta during the late heavy bombardment". In: *Icarus* 162, pp. 38–46 (page 207).

White, Rosalind V. and Andrew D. Saunders (2005). "Volcanism, impact and mass extinctions: incredible or credible coincidences?" In: *Lithos* 79.3, pp. 299–316. DOI: http://dx.doi.org/10.1016/j.lithos.2004.09.016. URL: http://www.sciencedirect.com/science/article/pii/S002449370400310X (page 188).

Wilkinson, Dave M. (1999). "Is Gaia really conventional ecology?" In: *Oikos* 84, pp. 533–536 (pages 27, 92, 109).

Wilkinson, David M. (2006). *Fundamental Processes in Ecology: An Earth Systems Approach*. Oxford University Press (pages 31, 65, 95, 142, 190, 207).

Williams, Angela (2008). "Turning the Tide: Recognizing Climate Change Refugees in International Law". In: *Law & Policy* 30.4, pp. 502–529. DOI: 10.1111/j.1467-9930.2008.00290.x. URL: https://doi.org/10.1111/j.1467-9930.2008.00290.x (page 233).

Williams, Hywel T. P. and Timothy M. Lenton (2007). "The Flask model: emergence of nutrient-recycling microbial ecosystems and their disruption by environment-altering 'rebel' organisms". In: *Oikos* 116.7, pp. 1087–1105 (pages 48, 49, 66, 68, 95, 109, 110, 113, 125, 153, 158, 165).

— (2010). "Evolutionary regime shifts in simulated ecosystems". In: *Oikos* 119.12, pp. 1887–1899. ISSN: 1600-0706. DOI: 10.1111/j.1600-0706.2010.18127.x. URL: http://dx.doi.org/10.1111/j.1600-0706.2010.18127.x (pages 48, 49, 66–69, 109, 110, 112, 113, 125, 153, 158, 165).

Williams, Hywel T.P. and Timothy M. Lenton (2008). "Environmental regulation in a network of simulated microbial ecosystems". In: *PNAS* 105.30, pp. 10432–10437 (pages 48, 49, 66, 68, 69, 109, 110, 113, 125, 153, 158, 165, 227).

Wilmers, Christopher C and Wayne M Getz (2005). "Gray Wolves as Climate Change Buffers in Yellowstone". In: *PLOS Biology* 3.4, e92–. URL: https://doi.org/10.1371/journal.pbio.0030092 (page 31).

Wilmers, Christopher C. et al. (2003). "Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA". In: *Ecology Letters* 6.11, pp. 996–1003. DOI: 10.1046/j.1461-0248.2003.00522.x. URL: https://doi.org/10.1046/j.1461-0248.2003.00522.x (page 31).

Wit, Julien de et al. (2016). "A combined transmission spectrum of the Earth-sized exoplanets TRAPPIST-1 b and c". In: *Nature* 537, 69 EP –. URL: https://doi.org/10.1038/nature18641 (page 148).

Wolf, Evan C., David J. Cooper, and N. Thompson Hobbs (2007). "HYDROLOGIC REGIME AND HERBIVORY STABILIZE AN ALTERNATIVE STATE IN YELLOWSTONE NATIONAL PARK". In: *Ecological Applications* 17.6, pp. 1572–1587. DOI: 10.1890/06-2042.1. URL: https://doi.org/10.1890/06-2042.1 (page 31).

Wood, A. J., G. J. Ackland, and T. M. Lenton (2006). "Mutation of albedo and growth response produces oscillations in a spatial Daisyworld". In: *Journal of Theoretical Biology* 242.1, pp. 188–198. DOI: https://doi.org/

10.1016/j.jtbi.2006.02.013. URL: http://www.sciencedirect.com/science/article/pii/S0022519306000786 (pages 161, 197).

Wood, Andrew J. et al. (2008). "Daisyworld: A review". In: *Review of Geophysics* 46.1 (pages 36, 43, 92, 158, 161, 173, 197).

Worden, Lee (2010). "Notes from the greenhouse world: A study in coevolution, planetary sustainability, and community structure". In: *Ecological Economics* 69.4, pp. 762–769 (pages 49–51, 153, 158, 166).

Worden, Lee and Simon A. Levin (2011). "A simple dynamic argument for self-regulation in model biospheres". In preparation (pages 49, 153, 158, 166).

Wordsworth, R. et al. (2013). "Global modelling of the early martian climate under a denser CO2 atmosphere: Water cycle and ice evolution". In: *Icarus* 222.1, pp. 1–19. DOI: https://doi.org/10.1016/j.icarus.2012.09.036. URL: http://www.sciencedirect.com/science/article/pii/S0019103512004290 (page 189).

Wordsworth, Robin and Raymond Pierrehumbert (2013). "Hydrogen-Nitrogen Greenhouse Warming in Earth's Early Atmosphere". In: *Science* 339.6115, p. 64. URL: http://science.sciencemag.org/content/339/6115/64.abstract (page 160).

Yang, Jun et al. (2014). "Strong Dependence of the Inner Edge of the Habitable Zone on Planetary Rotation Rate". In: *The Astrophysical Journal Letters* 787.1, p. L2. URL: http://stacks.iop.org/2041-8205/787/i=1/a=L2 (page 157).

Yeffeth, Glenn and H. G. Wells (2005). *The War Of The Worlds: Fresh Perspectives On The H. G. Wells Classic*. BENBELLA BOOKS (page 140).

Zahnle, Kevin, Laura Schaefer, and Bruce Fegley (2010). "Earth's Earliest Atmospheres". In: *Cold Spring Harbor Perspectives in Biology* 2.10, a004895. DOI: 10.1101/cshperspect.a004895. URL: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2944365/ (page 7).

Zahnle, KJ and NH Sleep (1997). *Comets and the Origin and Evolution of Life ed PJ Thomas, CF Chyba and CP McKay* (page 8).

Zsom, Andras et al. (2013). "Toward the Minimum Inner Edge Distance of the Habitable Zone". In: *The Astrophysical Journal* 778.2, p. 109. URL: http://stacks.iop.org/0004-637X/778/i=2/a=109 (pages 149, 157).